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COMITÉ DE RÉDACTION

J. D. CARTHY, P. H. CHRISTENSEN, A. C. COLE,
K. GÖSSWALD, P.-P. GRASSÉ, C. JUCCI,
A. RAIGNIER, D. STEINBERG, T. UCHIDA

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COMITÉ DE RÉDACTION

- J. D. CARTHY, Department of Zoology, Queen Mary College, Mile end Road, London E4 (England).
- P. H. CHRISTENSEN, Universitetets Institut for almindelig Zoologi, Universitetsparken 3, Copenhagen, Denmark.
- A. C. COLE, Department of Zoology and Entomology University of Tennessee, Knoxville, Tennessee (U. S. A.).
- K. GÖSSWALD, Institut für Angewandte Zoologie der Universität Würzburg, Röntgenring 10, Würzburg, Deutschland.
- P.-P. GRASSÉ, Laboratoire d'Évolution des Êtres organisés, 105, boulevard Raspail, Paris-VI^e, France.
- C. JUCCI, Istituto di Zoologia « L. Spallanzani », Pavia, Italia.
- A. RAIGNIER, 11, rue des Récollets, Louvain, Belgique.
- D. STEINBERG, Zoological Institute, Academy of Sciences of the U. S. S. R., Leningrad 164, U. S. S. R.
- T. UCHIDA, Zoological Institut Faculty of Sciences, Hokkaido University Sapporo, Japan.

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M. G. RICHARD

105, Boulevard Raspail, PARIS-VI^e

QUELQUES NOUVELLES REMARQUES SUR L'ÉTHOLOGIE
DE *POLYERGUS RUFESCENS* LATR.
(Hyménoptère, Formicidae).

par J. DOBRZANSKA et J. DOBRZANSKI
(Institut M. Nencki de Biologie Expérimentale, Varsovie).

Nous exposerons ici des recherches préliminaires qui nous ont permis de mieux connaître les *Polyergus* et de préparer nos recherches futures. La rareté de cette espèce et le peu de travaux qu'elle a suscités donnent quelque valeur à la présente note.

Le *Polyergus rufescens* est une espèce très rare. RUSZKIJ, excellent myrmécologue qui a réalisé d'importants travaux sur les fourmis de l'empire russe (1905), estimait que cette espèce n'existait pas en Pologne. KULMATYCKI a trouvé le premier nid de *Polyergus rufescens* en Pologne en 1922. PISARSKI en 1953 en a trouvé 4, nous en avons trouvé 6 dans les environs des Pulaves.

Tous ces nids étaient situés dans des endroits bien ensoleillés. Dans cinq nids, *F. Fusca* constituait l'espèce auxiliaire ; dans le sixième nous avons trouvé *F. Fusca* et *F. rufibarbis*.

Tout d'abord, il faut souligner la rigidité du comportement du *Polyergus rufescens* et son manque de plasticité.

Quand l'armée des *Polyergus* attaque un nid étranger, une partie des ouvrières attaquées transporte souvent les nymphes hors du nid et les dépose autour de l'orifice, pendant qu'une autre partie les emporte plus loin, en les sauvant ainsi de l'enlèvement. Grâce à cette division des fonctions, on voit se former autour de l'orifice un anneau de nymphes qui n'ont pas été encore évacuées. Les agresseurs ne leur prêtent aucune attention, bien qu'elles soient dépourvues de toute défense. Les soldats de *Polyergus* pénètrent au contraire dans le nid en les piétinant, et c'est seulement à l'intérieur du nid qu'ils enlèvent les nymphes restantes après avoir souvent dû livrer bataille en chemin.

L'armée des *Polyergus* ne s'arrête pas non plus si des nymphes, qui sont pourtant son but, sont déposées sur la route. Les soldats ne sont capables de les prendre qu'à la surface de leur propre nid (DOBRZANSKI, 1956). Leur instinct les fait envahir le nid étranger, et c'est uniquement à l'intérieur de ce nid qu'ils peuvent enlever leur proie.

Nous avons voulu étudier la manière dont l'expédition guerrière s'effectue. D'après l'opinion de FOREL (1874, 1923), ce sont des soldats spéciaux, « les éclaireurs », qui recherchent les objets de l'agression et conduisent ensuite toute l'armée. L'armée serait dirigée par des « officiers qui donneraient leurs ordres ». Ces ordres seraient transférés le long de la colonne de tête à tête. Nous n'avons jamais réussi à observer un tel phénomène. Quelques

expériences ont été effectuées pour vérifier l'existence des « éclaireurs » et des « officiers ».

Les expéditions des *Polyergus* s'accomplissent toujours l'après-midi pendant des jours bien ensoleillés. Comme le nid doit être en plein soleil, l'heure exacte dépend de son emplacement : un des nids se trouvait à l'ombre jusqu'à midi et, dans ce cas, les expéditions étaient toujours plus tardives. Quand le nid a été suffisamment chauffé par le soleil, il en sort quelques unités ou quelques dizaines d'individus qui s'éparpillent sur le terrain. L'expédition s'accomplit quelques heures plus tard.

A un certain moment on voit se déverser un torrent de fourmis qui tourbillonnent vigoureusement pendant quelques minutes à la surface du nid. Ensuite, on voit soudain le tourbillon prendre une certaine direction tout en s'étirant en une longue queue de 1 à 1,5 m de longueur et de 15 à 20 cm de largeur. La grandeur de la file dépend évidemment de la grandeur du nid et aussi du nombre d'expéditions qui ont déjà eu lieu ce jour-là. La première expédition rassemble le plus grand nombre d'individus, il est même possible que tous y prennent part.

Notre attention a été tout d'abord attirée par les individus qui sortent les premiers du nid. Étant donné que le *Polyergus* n'a pas de fonction ouvrière dans sa division du travail, le plus simple serait d'admettre que ces individus ont un rôle d'éclaireurs. Pour vérifier cette supposition, quelques individus ont été marqués et nous avons ensuite suivi pas à pas leur trace sur le terrain, en marquant tout leur chemin avec des jalons.

Nous avons observé ensuite si le retour d'un de ces présumés éclaireurs suscite la fièvre guerrière dans la colonie. Si oui, il faut encore prouver que l'armée va dans la même direction que l'éclaireur et que ce dernier a vraiment atteint le nid finalement attaqué. Dans quelques cas, l'armée est effectivement partie en expédition aussitôt après le retour d'un des éclaireurs, mais il n'est jamais arrivé que l'expédition se dirige dans la voie qu'il avait précédemment suivie, et il n'a jamais joué le rôle d'un guide direct.

Nos conditions ne nous ont pas permis d'observer tous les individus sortis du nid avant l'expédition, et il se peut que l'attaque ait été provoquée par une fourmi qui a échappé à notre attention. Pour exclure cette possibilité, nous avons décidé de séquestrer toutes les fourmis qui sortent individuellement du nid, ce qui est possible, car la quantité des orifices d'un nid de *Polyergus rufescens* n'est pas trop grande. Malgré cette élimination des éclaireurs potentiels, les expéditions s'effectuent sans aucun trouble. On aurait pu supposer que l'armée était encore dirigée par les éclaireurs des jours précédents. Nous avons donc éliminé ces fourmis pendant quelques jours de suite et au bout de ce délai, les éclaireurs ont cessé d'apparaître. Il en résulte donc qu'ils constituent un groupe constant d'individus et, dans un grand nid, leur nombre atteint environ 80. Malgré cette élimination complète des prétendus éclaireurs, les expéditions guerrières s'effectuent sans aucun trouble. La conclusion qui s'impose c'est que ce groupe d'individus ne joue pas le rôle qu'on lui supposait dans les expéditions guerrières. La question se pose dans ce cas, de connaître la raison de leur comporte-

ment. Ce sont peut-être les individus qui ont le mieux conservé l'instinct atavique de recherche sur le terrain, tout en perdant la possibilité de récolte de matériaux.

On aurait pu supposer que les caractéristiques de division du terrain de récolte démontrées pour le genre *Formica* par DOBRZANSKA (1958) étaient valables aussi pour les amazones chez qui on aurait trouvé alors une division du terrain de pillage, mais cette hypothèse n'a pas été confirmée : les mêmes individus participent aux expéditions effectuées dans différentes directions.

Dans un autre groupe d'expériences, nous avons voulu résoudre le problème de l'existence des « officiers » qui commanderaient la colonne.

Dans ce but, nous avons marqué la tête de la colonne et observé dans la suite son comportement. Il s'est avéré que la notion de tête de la colonne est tout à fait instable : les individus marqués sur le front de progression sont bientôt dépassés par d'autres individus qui, marqués à leur tour, sont eux aussi distancés et se dispersent le long de la colonne. Leur comportement ne les distingue en aucune manière du reste des guerriers. Les mêmes mouvements se répètent si on marque les fourmis de tête une troisième fois avec une autre couleur. Nous avons aussi séquestré toute la tête de la colonne, ce qui n'a exercé aucune influence sur le reste de l'armée, qui, sans hésitation, a continué sa marche dans la même direction. Nous pouvons donc affirmer que ni les « officiers », ni les « éclaireurs » ne dirigent la colonne des *Polyergus*. Il nous semble que d'autres éléments règlent sa direction et son comportement.

Pour savoir si le chemin de l'armée est déterminé d'avance, nous avons posé des nids artificiels de fourmis auxiliaires sur l'itinéraire de la colonne. Pour cela, nous avons déterré un nid de *F. Fusca* et nous l'avons installé avec sa terre dans un cristallisoir un jour auparavant pour qu'il puisse s'habituer. Au moment où la direction de la colonne des *Polyergus* fut précisée, nous avons enterré le cristallisoir, et répandu un peu de terre du nid autour. La réaction de la colonne au nid artificiel est très originale et inattendue. La colonne s'arrête, se disperse par groupes et, pendant quelques minutes, demeure complètement immobile, sans aucun signe d'entente réciproque. Cet état d'immobilité est tout à fait inattendu pour cette espèce si animée et si rapide. Après un certain temps, la colonne se remet en marche et retourne dans son propre nid ou continue son expédition en contournant le nid artificiel. Quelques individus tout au plus pénètrent dans le nid et emportent quelques nymphes. Dans un cas où le nid artificiel a été placé très près du nid des *Polyergus*, ce sont des « esclaves » de l'espèce *F. Fuscas*, qui ont pénétré dans le cristallisoir et enlevé les nymphes.

Nous expliquons ce comportement du *Polyergus* par son manque exceptionnel de plasticité. Il nous semble que l'armée est désorientée par l'apparence artificielle de ce nid. Malgré la terre dispersée autour du cristallisoir, le nid n'a pu acquérir l'intensité naturelle ni les gradients des odeurs ; les voies internes du nid n'ont pas eu le temps de se constituer normalement. Étant donné que le *Polyergus* est incapable d'enlever les nymphes se trou-

vant sur son chemin ou aux abords du nid attaqué, on peut conclure que les conditions du nid artificiel ne sont pas assez typiques pour provoquer l'agression ; au contraire, cette situation a troublé le cours normal de l'expédition.

Les expériences décrites et certaines observations nous ont fait conclure que le *Polyergus rufescens* n'a pas d'officiers et que le mouvement de la colonne s'effectue sans dirigeants.

Après avoir obtenu ces résultats uniquement négatifs, nous avons entrepris des observations plus détaillées ; les résultats sont les suivants :

Dans les heures matinales, des individus isolés sortent et circulent à une assez grande distance du nid, ce sont les prétendus éclaireurs. Ils retournent au nid pour la plupart avant midi, quelquefois un peu plus tard.

Une heure environ avant le commencement de l'expédition des amazones, d'autres individus sortent du nid. Ces derniers sont plus vifs. ils courent hors du nid et y reviennent, ne s'éloignant que de 1 à 3 m. A cause de leur rôle établi par la suite, nous les avons appelés des « activateurs ».

Le rassemblement d'une grande quantité d'activateurs dans une direction suscite une agitation croissante et attire de plus en plus d'activateurs dans cette même direction, peut-être par « kinopsis » (STAGER, 1931). Certains d'eux rentrent pour un instant dans le nid mais en sortent de nouveau tout de suite. Après quelques minutes de cette circulation accrue des activateurs, on observe nettement le moment où les masses de soldats débouchent littéralement de tous les orifices du nid. Ces soldats se jettent le plus souvent presque immédiatement vers le lieu de concentration des activateurs. Dès alors, la direction de l'expédition est déterminée. L'armée ira maintenant tout droit sans tenir compte des obstacles, et ce n'est que rarement qu'elle déviara de la direction choisie.

La tête de la colonne étant très fluctuante ainsi que nous l'avons signalé, on ne peut pas la définir de façon précise, mais les activateurs se retrouvent plutôt dans la première partie de l'armée que vers la queue, où se rencontrent des fourmis plus lentes qui souvent retournent au nid à mi-chemin.

L'expérience suivante consistait à éliminer les activateurs. Bien qu'il soit difficile de les éliminer complètement, les résultats des expériences sont nets : l'élimination de la majorité des activateurs supprime l'expédition des amazones par disparition de la première phase de l'attaque, c'est-à-dire, la sortie massive des soldats.

Pour savoir si l'agitation accrue des activateurs avant l'expédition est bien la cause déterminante de la direction de l'attaque, nous avons déplacé des activateurs dans une direction où il n'y en avait que très peu. Nous avons réussi quelque fois de cette façon à provoquer une expédition dans la direction choisie. Ces résultats n'étaient pas suffisamment nets pour nous permettre d'éliminer entièrement des causes accidentelles. En tout cas, cette dernière expérience permet de rejeter l'éventuelle objection que, dans les expériences où on élimine les activateurs, l'expédition n'a pas lieu à cause de la perturbation que l'on a provoquée. Sans doute le déplacement

d'une masse d'individus cause une perturbation plus importante, mais, dans ce cas, l'expédition n'est pas paralysée.

Il est donc hors de doute que ce sont ces activateurs, plus vifs et plus excitables, qui déclenchent l'excitation dans le nid et stimulent toute l'armée des amazones à l'attaque. C'est probablement aussi leur mouvement qui détermine la direction de l'expédition.

Nos observations suivantes ont eu pour but de connaître les raisons du choix de cette direction.

Nous avons très longtemps observé un nid de ce point de vue. Successivement pendant trois jours l'armée de ce nid a attaqué toujours le même nid de *F. rufibarbis* jusqu'à la destruction complète de celui-ci.

Le troisième jour, pendant que l'armée se dirigeait de nouveau vers le même lieu, où il ne restait que les ruines du nid démoli, une partie des agresseurs dévia par rapport à cette direction et, contournant le nid déjà pillé, elle trouva un nouveau nid de *F. fusca*, qu'elle attaqua aussitôt. Le jour suivant, toute l'armée s'en alla dans la nouvelle direction qui fut alors conservée pendant quelques jours.

Au fur et à mesure de la mise à sac des nids voisins, l'armée s'éloignait de plus en plus dans cette direction. La dernière expédition s'avança jusqu'à 80 m mais sans succès : la colonne ne trouvant pas de nid sur son chemin, retourna au nid sans capture. Le jour suivant, la direction fut changée et l'armée la conserva de nouveau pendant quelques jours en s'éloignant de plus en plus.

Cette observation, comme le fait que, très souvent, l'armée de *Polyergus* n'ayant pas trouvé d'objet d'attaque retourne au nid sans butin, nous fait penser que le choix d'une certaine direction est accidentel. Si la direction s'avère efficace, c'est-à-dire, si elle est renforcée par un stimulus inconditionnel — les nymphes étrangères — elle s'affermir et sera conservée pendant un certain temps jusqu'au pillage complet du terrain. Dans ce cas, la direction ne sera plus alors renforcée par les nymphes étrangères et il y aura, au contraire, inhibition du comportement orienté dans cette direction.

Après cela, la nouvelle voie de déplacement sera la résultante des différentes directions choisies par la masse des activateurs qui tourbillonnent autour du nid avant le début de l'expédition.

Notre hypothèse est confirmée par les travaux de Raignier et V. Boven (1955), avec le genre *Anomma*. Ces auteurs affirment que la direction de la colonne de ce genre nomade et guerrier est la résultante des différentes directions choisies par quelques groupes de fourmis.

Voici encore une intéressante observation : Observant les nids mixtes de *Polyergus rufescens* et de *Formica fusca*, nous avons remarqué que les ouvrières *F. fusca* deviennent très agressives dans ces conditions. Leur activité guerrière augmente beaucoup, surtout pendant l'expédition des *Polyergus rufescens* ou même quand ces derniers circulent en masse autour du nid. On peut alors observer, par exemple, quelques *F. fusca* qui se jettent sur une ouvrière *F. sanguinea* et la quittent seulement après l'avoir tuée. Nous avons aussi remarqué des *F. fusca* qui prenaient part à la lutte avec

des *F. sanguinea* au côté de *Polyergus*. Un tel comportement de *F. fusca*, tout comme le fait déjà mentionné, que cette fourmi enlève les nymphes d'un nid étranger sont inimaginables dans le cas d'un nid normal de cette espèce. Dans des conditions normales, cette espèce est très paisible, ce qui n'est pas le cas de *F. rufibarbis*, qui se défend toujours contre les attaques des *Polyergus*. Nous n'avons jamais vu *F. fusca* se défendre contre des attaques de ce genre. Sa réaction normale est de s'enfuir. Le système de construction de son nid nous montre déjà son caractère : les nids sont toujours très bien camouflés et presque invisibles.

Le comportement des ouvrières de *F. fusca* est donc changé par leur séjour dans un nid étranger.

Forel (1923) et Wilson (1955) affirment que les ouvrières esclaves conservent dans un nid étranger le comportement caractéristique de leur espèce. Cette observation est juste en ce qui concerne leur comportement en général (la construction du nid, la nourriture, etc...), mais, dans certains domaines, comme celui que nous venons de décrire, leur comportement change sous l'influence des conditions spécifiques. Il serait intéressant d'étudier ce qui cause ces changements. Nous voyons deux possibilités : l'imitation (si elle a lieu chez les fourmis en général) ou des causes de nature hormonale. Ces dernières demanderaient des recherches biochimiques.

Transport mutuel des ouvrières attaquées par des *Polyergus rufescens*. — HUBER (1810), OKLAND (1931) associent le phénomène du transport mutuel des ouvrières, uniquement avec le déménagement de la colonie. Nous avons obtenu de nouveaux résultats en étudiant la réaction des espèces *F. fusca* et *F. rufibarbis* à l'attaque des *Polyergus rufescens*.

Pendant l'attaque, une partie des ouvrières défend le nid, une autre s'enfuit en emportant les nymphes ; entre ces dernières se trouvent aussi des ouvrières de coloration claire, donc très jeunes.

Elles se cachent par groupes sous des feuilles, des racines, etc... à une distance d'un mètre, un mètre et demi du nid. Après l'attaque, un nombre constant d'ouvrières ramène systématiquement les nymphes au nid. Elles y transportent aussi les jeunes ouvrières, qui sans leur aide, seraient incapables de revenir : c'est leur première sortie et elles n'auraient certainement pas retrouvé le chemin de retour.

Les mêmes résultats peuvent être obtenus artificiellement par la destruction partielle du nid.

La fonction de transport a donc une importante signification en tant que défense contre la perte des jeunes ouvrières en cas de péril.

Nous avons été intéressés par le fait que les jeunes ouvrières ont la faculté de prendre la position la plus commode pour faciliter le transport. Nous avons vérifié ce fait avec d'autres espèces dans des élevages. Quand nous prenions en main des ouvrières de *F. sanguinea* fraîchement écloses pour les marquer, certaines d'entre elles (nous avons observé cinq cas) se pelotonnaient dans la main d'une façon caractéristique semblable à celle prise par les individus du genre *Formica* pendant le transport. La faculté de

prendre une certaine position pendant le transport doit être donc innée et possède une importante signification d'adaptation. Il nous semble que cette faculté joue un rôle important avant tout dans le cas où le nid est brusquement menacé. Un déménagement normal se déroule en quelques jours ou même quelques semaines (OKLAND) et, dans ce cas, une telle adaptation ne peut avoir une signification importante pour l'espèce.

Summary

According to our observations and experiments there are no special individuals (named scouts by Forel) whose task it would be to find the object of the attack.

In the nest there exists a small number of individuals, who are rambling in the ground before noon. If those individuals are removed from the ground, this has no effect on the raids of the amazons. However the raid will not take place if we withdraw most of the individuals, which are called by us the activators. They come out of the nest about an hour before the beginning of the raid and by their excitation they provoke the other amazons to get in mass out of the nest. This mass immediately goes forward for the attack in that direction, where the most of activators are actually. Afterwards the column is progressing without the guidance of anybody. Removing of the head of the column has no influence on the course of the raid. Besides, specimen composition of the head of the column is constantly varying.

Zusammenfassung

Unsere Beobachtungen und Erfahrungen verneinen, dass die Raubzüge von Amasonenameisen durch bestimmte Individuen gelenkt wären, welche zuvor die Objekte ausgesucht hätten sollen, und welche Forel die Kundiger genannt hatte.

In Wirklichkeit existieren im Neste manche Individuen, welche vormittags einsam die Umgebung betreten und besuchen. Eine vieltätige und strenge Eliminierung solcher Individuen stört jedoch keinesfalls die Raubzüge der Amasonenameisen. Die Raubzüge kommen aber nicht zum Stande, wenn nimmt man einen grösseren Teil der Individuen ab, welche von uns « die Aktivisten » genannt sind. « Die Aktivisten » gehen aus dem Neste etwa eine Stunde vor dem Zuge heraus, und wegen seiner Aufregung rufen einen schaarenweisen Ausgang aus dem Neste der übrigen Amasonenameisen heraus. Diese Heermasse rückt sofort in dieser Richtung aus, in welcher aktuell die meisten « Aktivisten » sich befinden. Nachher geht die ganze Armee ohne Lenkung gerade vor sich. Die Eliminierung der Spitze der Amasonenarmee übt keinen Einfluss auf den Verlauf des Raubzuges; übrigens es erwies sich, dass diese Spitze besitzt keinen konstanten Individuenbestand.

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CASTE IN THE HONEY BEE

by Stanley E. FLANDERS

(University of California Citrus Experiment Station, Riverside)

The differentiation of caste in the honey bee (*Apis mellifera*) is an effect of the food received during larval life (Weaver, 1957). This differentiation, however, appears to be dependent on the newly hatched larval female being predisposed to become a worker not a queen, the queen being subsequently derived from a larval worker by special feeding. That this is the sequence by which the female of the honey bee becomes a queen is implied by Snodgrass (1956) in his conclusion that the "magic formula" fed to the young female "must contain a specifically inhibitory ingredient as well as an excess of some ovarial stimulant." In such a case the widely held opinion that the worker caste in the social Hymenoptera is initiated during larval growth would not be valid.

That the disposition of the individual to be a nonreproductive adult is prelarval rather than larval is indicated by the fact that in many Hymenoptera the amount of food consumed during larval development may vary as much as 10-fold without affecting the basic reproductivity of the resultant females. One female may be 10 times the size of another, but differ reproductively only in the number of eggs generated (Flanders, 1935 a). The quality of food consumed by the larvae of such Hymenoptera may affect the morphology of the adult but not its basic reproductivity (Schneider, 1938).

The need for a "magic formula" is limited to the species of social Hymenoptera characterized by systematized differential feeding of the larvae, a phenomenon correlated with an inability to produce reproductive females irrespective of the amount and/or quality of larval food. In such species, the development of a queen or worker from a fertilized egg is facultative. This is the case with the honey bee and the army ant (Flanders, 1957 ; Schneirla and Brown, 1952).

In the stingless bees (*Melipona* spp.), differential feeding of the larvae does not occur, consequently they possess the capacity to produce queens and workers irrespective of differences in the amount or quality of larval food (Wheeler, 1928). In such species the development of either a queen or a worker from a fertilized egg is obligatory; the queen being derived from a fully nourished embryo, the worker from a partially nourished embryo which in its subsequent larval stage rarely if ever receives queen-producing food. It seems therefore that in the species in which the

development of the queen from the fertilized egg is facultative and colonial life is characterized by a systematized differential feeding of the larval brood, all the newly hatched female larvae are predisposed to become workers.

The annual societies of the halictid bees may present systematized feeding in a more primitive form, the larval summer progeny of the queen receiving less food than her larval autumn progeny.

It is possible, however, that in the Halictinae the development of a queen from a fertilized egg is obligatory rather than facultative. This is likely to be the case in primitive social forms in which the polymorphism of the female is slight or lacking. The occurrence of the queens only in autumn may result from the deposition of fully nourished fertilized eggs, the deposition of such eggs resulting from the queen being relieved of all colony duties excepting egg production. A high proportion of the eggs could then be deposited before being subjected to the process of ovisorption.

In the species of social Hymenoptera in which the development of a queen from a fertilized egg is facultative, the sex ratio seems to be determined only by the sensitivity of the queen's spermathecal gland to external stimuli. Michener and Lange (1958), noting in the Halictinae a correlation between the size of the adult female and the production of males, suggested that size and sex ratio were controlled in some way by the weather. Such control was reported by Schneirla and Brown (1952) with the army ant. In species in which queen development is obligatory, the sex ratio seems to be largely an effect of the rate of oviposition in conjunction with the capacity of the spermathecal gland to secrete sperm-activating fluids (Flanders, 1946).

Differential feeding is accomplished in the honey bee by the different dimensions of the brood cells, in the army ant (*Eciton*) by the worker population destroying a major portion of the eggs of one the periodic broods, a procedure correlated with exceptionally dry conditions during egg deposition. The development of a "dry" army ant brood is relatively rapid despite the greater size of the individual ant. The uneaten fertilized egg becomes a queen, presumably an effect of the addition of egg material to the diet of the larval instars and the consumption of a greater proportion of the collected "booty" (Schneirla and Brown, 1952).

It is obvious that in the honey bee the quantitative differences in the nutrition of the larval worker and the larval queen (small relative to such differences in the larval nutrition of nonsocial Hymenoptera) is very effective in regulating the occurrence of castes, the basis for such effectiveness being presumably the predisposition of the newly hatched larva to become a worker; a predisposition readily counteracted nutritionally during larval development. The proportion of the brood yielding reproductive adults is determined by colony structure, this structure being adapted for the production of the few larvae needed for queens and for the specialized nutrition and extra feeding of these.

The predisposition of the larva to become a worker is apparently

initiated in the egg by a reduction in the amount of yolk prior to ovulation. Bier (1954), working with the ant *Formica rufa*, demonstrated the relation of yolk reduction in the ovarian egg to the predisposition of that egg to become a worker. The undernutrition of the embryo as the predisposing factor was suggested 20 years ago by the experiments of Goetsch (1939) in which he transferred the eggs of ants from one colony to another. It is significant that Goetsch also demonstrated by using *Pheidole pallidula* that the realization of the soldier caste is restricted to worker larvae which, before they are 6 days old, are fed with a growth ingredient which may be derived from the bodies of termites.

The ovarian mechanism involved in the reduction of yolk and the initiation of the worker caste appears to be the ovisorption process, a process which is common to all Hymenoptera in which ovulation is externally induced and oviposition highly specialized (Flanders, 1935 *b*, 1946, 1950, 1953).

With the honey bee the incubation of the egg begins when it is in the ovary of the queen and ends when it is in the brood cell. All the ovarian eggs at the beginning of incubation or at the moment of egg maturity are supposedly identical, one with another. Nevertheless, each egg can become either a worker, drone or queen. Since the incubation of the honey bee is a continuous process (the assumption that nuclear activity can be suspended during meiosis (Tucker, 1958), appears unwarranted), its disposition either by deposition or by absorption is essential for the normal functioning of the parent queen. Ovulation is followed almost immediately by oviposition. Each egg, as it passes along the common oviduct of the queen, usually is fertilized, provided that activated sperms are present in the sperm duct (Flanders, 1946).

From the standpoint of the individual, the incubation of the egg is the critical period in which the course of its development is determined. It is in the egg that the inherent predetermination of the individual to be a male can be changed (by fertilization) so that it becomes a female, and the inherent predetermination of the female to be a reproductive changed (by undernutrition) so that it can become a worker. It has been suggested (Tucker, 1958) that the occasional development of a female from an unfertilized egg may be brought about by the egg being retained in the ovary for a certain length of time.

The egg of a normal queen at the moment of its deposition usually contains an amount of yolk sufficient for the complete development of either the male or female embryo. In the case of the fertilized egg a reduced amount is considered essential for its predisposition to become a worker. It appears to have no such effect on the developmental course of the male from the unfertilized egg presumably because of the male's relatively low nutritional needs.

In this connection it may be significant that the egg of the honey bee, from the moment of its deposition to that of hatching, loses nearly one-third of its original weight, dropping from 0.132 mg. to 0.09 mg. (Melampy

and Willis, 1939). This loss in weight may represent the loss of water which had replaced the yolk extracted by the ovisorptive process.

The probability that the predisposition of every fertilized egg to become a worker results from the undernutrition of the embryo is greatly enhanced by instances of a healthy queen depositing all of her eggs in a normal manner but with the embryos in most, if not all, of the eggs unable to complete their development.

Limited embryonic development is characteristic of the defective hymenopterous egg (Hitchcock, 1956; Whiting, 1940). In all species of Hymenoptera in which ovulation is externally induced, the deposition of a defective egg may often occur (Hase, 1922; Smith, 1932; Rosenberg, 1934), the cause being, as suggested by D. J. Jackson (1937) 20 years ago, its regression before ovulation.

It is significant that the nectar and pollen from the California buckeye (*Aesculus californicus*), if fed to the queen honey bee in a small amount, results in egg deposition at a reduced rate, with each egg, although normal in appearance, either failing to hatch or yielding a larva that soon dies (Eckert, 1933).

It is logical to assume that the death of embryos in deposited eggs that are normal in appearance is an effect of such eggs having been retained in the ovary until so much of the yolk was extracted that the amount remaining was not sufficient for the completion of embryonic development.

The fact that the composition of the ovarian egg may change in the interval between its maturity and its deposition (Flanders, 1942), correlated with the fact that in the defective larvae from such eggs the life of the male is slightly longer than that of the female (Mackensen, 1951), indicates embryonic starvation as the cause of the defective hymenopterous egg (Flanders, 1959). The difference in the longevity of the defective male and female larvae noted in the honey bee is probably dependent on the nutritional needs of the male being less than those of the female rather than on any modification of the genetic make-up. Aging of the queen is known to cause the proportion of defective eggs to increase (Hitchcock, 1956).

When the ovarian loss of yolk is not excessive, the egg, if fertilized, possesses the capacity to develop either into a worker or a queen.

The Counteraction of the Predisposition to Become a Worker.

At the beginning of postembryonic development all individuals are presumably more or less equal in their capacity for growth, yet healthy larvae, when provided with excess food, show when three days old a wide divergence in individual weights (Melampy and Willis, 1939), an effect, possibly, of differences in the amount of yolk retained in the egg.

The individual female recovers its capacity to become a queen only as a young larva in a queen cell. This recovery, which may be well under way before the second day of larval life (Melampy and Willis, 1939), is

apparently initiated when the larva receives a substance of special quality prior to its attaining a weight of 35 mg. (Rhein, 1933). This substance appears to be most effective when the larva is three days old. Such a larva, however, as Haydak (1943) showed with starved individuals, can complete its development into a queen only when it receives an amount of food that will enable it to attain, at the time that it forms its cocoon, a weight in excess of 230 mg.

The successful development of the reproductive female in the honey bee apparently involves two steps: first, the special nutrition of a female larva less than four days old; and second, the adequate extra feeding of the larva throughout its later stages. This conclusion is derived from the experiments of Rhein (1933) and of Weaver (1957), experiments which show that the reproductive caste is initiated by the qualitative feeding of the larvae before they are three and one-half days old, subsequent quantitative feeding, however, being essential for their complete development as reproductives. Weaver, in fact, concluded that the tendency of the worker larva to become a queen is irreversibly established during its second and third days of life, provided that during that period it is in a queen cell which is within an environment suitable for queen rearing.

In his study of dimorphic differentiation, Weaver, when transferring queen larvae that were more than three days of age to worker cells, had to place them in either enlarged worker cells or in drone cells because at that age they were so large that it was difficult or impossible to crowd them into a worker cell and have their position normal. He noted that as a rule any female larva which had been exposed in a queen cell for a two-day period beginning at the start of its third day of life usually was not accepted by the bees when placed in a worker cell. Nonacceptance of queen larvae in worker cells by the bees may be correlated with the food supply being inadequate or the inherent minimum size of the larval queen being greater than the space available. Weaver found that the nurse bees are able to distinguish between queen and worker larvae that are less than two and one-half days old, and that they remove the larvae of one caste from the cells of the other.

Summary.

The known facts concerning the physiology of the honey bee and of other social Hymenoptera physiologically similar indicate that when the ovulated egg has a reduced amount of yolk it is disposed to become a worker and does so if it is fertilized and the worker character of the resultant larva is not nutritionally counteracted. Queen production from fertilized eggs, therefore, is facultative. According to this concept the system of differential larval feeding which characterizes the life of the honey bee does not initiate the worker caste. It is a system by which the worker bees regulate caste ratios with very few of the worker larvae being transformed

into queens. In this transformation of the female, the "primitive" queen status is recovered through Snodgrass' "magic formula," a formula involving extra qualitative and quantitative nutrition. This recovery appears to be irreversibly established by qualitative feeding during the second and third days of larval life.

Résumé.

D'après nos connaissances actuelles sur la physiologie de l'Abeille, nous pouvons affirmer que la condition d'ouvrière n'est pas déterminée par la nourriture reçue à l'état larvaire. Les larves femelles récemment écloses sont en effet prédisposées à devenir ouvrières ; la reine pourra se développer plus tard à partir d'une de ces larves, mais en recevant une nourriture spéciale. La transformation de la larve d'ouvrière en reine se fait sous deux influences :

- une influence qualitative de la nourriture qui se manifeste pendant les 3 1/2 premiers jours de la vie larvaire ;
- une influence quantitative de la nourriture (accroissement), qui agit pendant toute la vie larvaire. Il semble bien que ce soit la faible quantité de vitellus accumulée pendant l'otogenèse qui caractérise l'œuf d'ouvrière. L'élevage de la reine nécessite justement un apport important de nourriture pour compenser cette faible réserve vitelline de l'œuf.

Zusammenfassung.

Nach unsere Kenntnissen über die Physiologie der Honigbiene wird die Entstehung der Arbeiterkaste, wie sie für den Bienenstaat charakteristisch ist, nicht durch differenzierte Fütterung der weiblichen Larve eingeleitet. Die larvale Verschiedenheit der Kaste beruht offenbar auf der Prädisposition der frisch geschlüpften weiblichen Larve zur Arbeiterin, wobei die Königin später durch besondere Ernährung aus einer Arbeiterinnen-Larve hervorgeht. Die Umwandlung von der Arbeiterinnen-Larve in eine Königin erfolgt in zwei Stufen, zunächst der qualitativen Beeinflussung der Ernährung während der ersten 3 1/2 Tage des Larvenlebens, sodann ist eine Erhöhung der Nahrungsmenge erforderlich. Die Prädisposition des Eies zur Arbeiterin wird durch Reduktion der Dottermenge vor der Ovulation verursacht.

Von diesem Zeitpunkt an geht die Disposition des Eies zur Königin verloren. Die Disposition zur Königin kann jedoch später von der weiblichen Larve wiedergewonnen werden, wenn diese geeignete Nahrung erhält.

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STUDIES ON THE POLYMORPHIC WORKERS OF THE ARMY ANT *DORYLUS (ANOMMA) NIGRICANS* ILLIGER

by M. J. HOLLINGSWORTH

(University College of Ghana, Legon, Ghana.)

Introduction.

The workers of the army ants have been studied from several aspects by previous workers.

Raignier and van Boven (1955) have described details of the behaviour of the workers on their foraging expeditions and on their migrations from one nesting site to another. They were particularly concerned with *Dorylus (Anomma) wilverthi* Emery. Huxley (1927) first studied the size variation in the workers of *Anomma nigricans* from the point of view of the association between polymorphism and allometry.

Cohic (1948) has given an account of the morphology and polymorphism of the workers of *Anomma nigricans*. He claimed that the workers could be divided into distinct morphological and functional types. It is largely to refute Cohic's conclusions that the present paper has been written. It will be shown that although there is an extreme size variation there is no morphological or functional discontinuity in the workers, and that they can be placed in a continuous series from the smallest to the largest.

Material.

The material was from two sources. In April 1958 my bungalow was invaded by a column of foraging ants. They emerged from the bush and continued to pass by my bungalow for a day and a night. The activity of the workers never ceased, although it fell off during the heat of the day. At first all the workers travelled in one direction out of the bush. Later, some of them were seen travelling back into the bush in the direction from which they came. Many of these were carrying captured food. In the final stages all the workers were travelling back into the bush. Similar foraging expeditions have been described in detail by Raignier and van Boven (1955) in the related species *Anomma wilverthi*.

An *Anomma nigricans* nest was discovered beneath a compost heap about 400 yards from my bungalow at a later date. The nest was opened at midday when the activity outside the nest was at a minimum. My assistant and I managed to open the nest and to collect some eggs, larvae, prepupae and pupae, as well as workers, but the activity of the workers forced us to give up an attempt to find the queen. It is quite likely that the foraging expedition described above came from the same colony that was found in the nest.

The morphology of the workers.

The workers of *Anomma nigricans* vary greatly in size. The largest worker in the sample obtained (Fig. 1 *a*) was 12.3 mm. long excluding the mandibles, and the smallest (Fig. 1 *c*) 2.5 mm long. The largest is therefore nearly five times as long as the smallest. However, a linear measurement does not reflect the true difference in size. An attempt was made to measure their volume as it was impossible to weigh the smallest ants with the apparatus available. This was done with a micrometer syringe

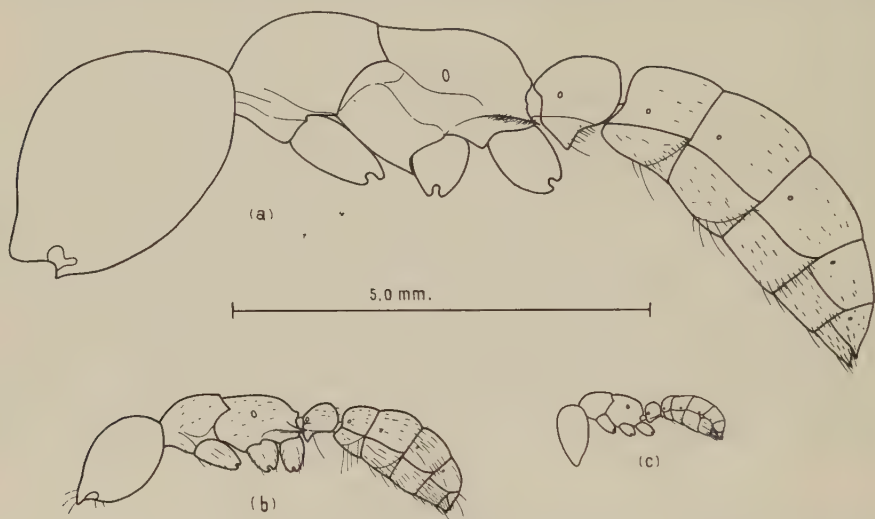


FIG. 1. — Lateral views of the workers of *Anomma nigricans* with legs, antennae and mandibles removed.

(*a*) the largest individual found, from the 300-309 unit class; (*b*) a medium sized individual, from the 110-119 unit class; (*c*) the smallest individual found, from the 50-59 unit class.

fitted to a capillary tube in which the ant was placed. The largest ant had a volume of 0.03 ml. and the smallest a volume of 0.0004 ml. The largest ant is therefore about 75 times the volume of the smallest.

The ants can be arranged in a continuous series from the largest to the smallest. When this is done it is seen that there is a change in shape with change in size. This is particularly noticeable in the head.

All the ants are not of the same colour. Most are very dark brown. The largest are almost black. The smaller ants are less darkly pigmented than the others. The smallest are golden brown.

The workers of *Anomma nigricans* resemble those of the related species *A. wilverthi*. Two ways in which they differ are in the shape of the head and in body colour. The head of *Anomma wilverthi* has a backward pointing projection at each posterior angle of the head, this being most marked in the larger individuals, whereas the posterior angles of the head in *A.*

nigricans are rounded. Consequently the head of *Anomma wilverthi* is relatively longer than that of *A. nigricans*. The workers of *Anomma wilverthi* are of a lighter, more reddish-brown than those of *A. nigricans*.

The head—The head of the large workers is massive. That of the largest individual in the sample collected was 3.5 mm. wide, 3.3 mm. long and 2.3 mm. high. That of the smallest was 0.6 mm. wide, 0.7 mm. long

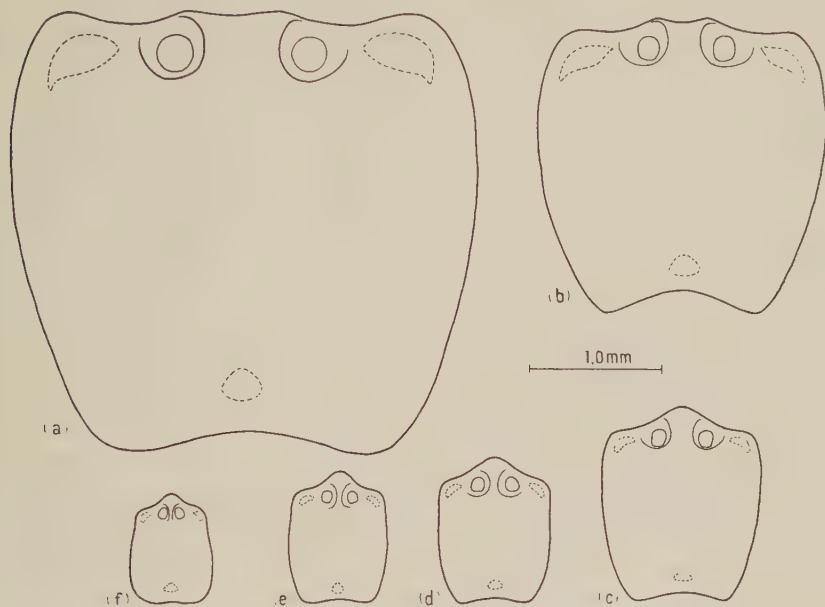


FIG. 2. — Dorsal views of the head capsules of different sized workers of *Anomma nigricans*, with antennae and mandibles removed.

(a) the largest individual, from the 300-309 unit class; (b) from the 200-209 unit class; (c) from the 120-129 unit class; (d) from the 90-99 unit class; (e) from the 70-79 unit class; (f) the smallest individual, from the 50-59 unit class.

and 0.4 mm. high. It can be estimated from these measurements that the volume of the head of the largest worker is about 150 times that of the smallest. The head of the largest worker is relatively higher and wider than that of the smallest. This change in proportions is associated with the relatively greater size of the mandibles in the larger forms. This is shown in Figure 2.

The head of the smallest workers is widest posteriorly. The position of the widest point passes anteriorly with increase in absolute size of the head. The clypeus of the smallest workers is very prominent. It becomes less prominent with increase in size of the head, and it is indented in the largest individuals. The frontal carinae do not overlap the antennal insertions in any worker. They diverge posteriorly and come to encircle the antennal insertions more completely as the head increases in size.

The antennae are inserted close to the anterior margin of the head towards the mid-line. They extend no more than one third of the distance from the mid-line to the lateral margin of the head in any individual.

The mandibles are inserted laterally on the ventral surface at the anterior margin of the head, which is very prominent in the largest workers.

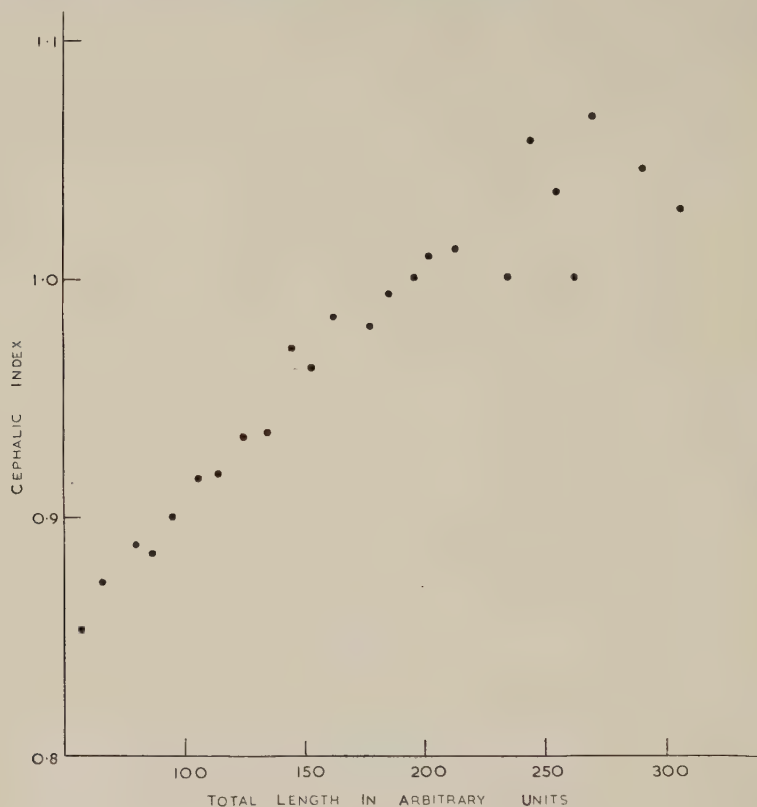


FIG. 3. — The cephalic index of different sized workers of *Anomma nigricans*. Cephalic index = mean maximum width/mean maximum length.

The neck is inserted ventrally in all workers. The majority of workers are prognathous. Only the smallest workers are hypognathous. The former condition is probably associated with the functions of the mandibles, which are seizing and cutting prey and enemies.

The shape of the head of the workers of the related species *Anomma wilverthi* has been expressed in terms of a cephalic index (greatest width/greatest length) by Raignier and van Boven (1955). They showed that this index increases with absolute size. The cephalic index of *Anomma nigricans* workers of different sizes is illustrated in Figure 3.

The head is smooth except for fine sculpturing. Bristles are absent except for a few round the mouthparts. Eyes and ocelli are completely absent.

The antennae consist of a slightly curved scape and a 10-segmented funicle in all but the smallest workers. The segments of the funicle are all longer than wide in the larger individuals. But the number of segments may be as few as seven and many of these may be wider than long in the smallest workers.

The antennae may be placed in a series (Fig. 4) which illustrates the reduction in the number of segments with decrease in size. The reduction in the number of segments takes place in the following stages. First,

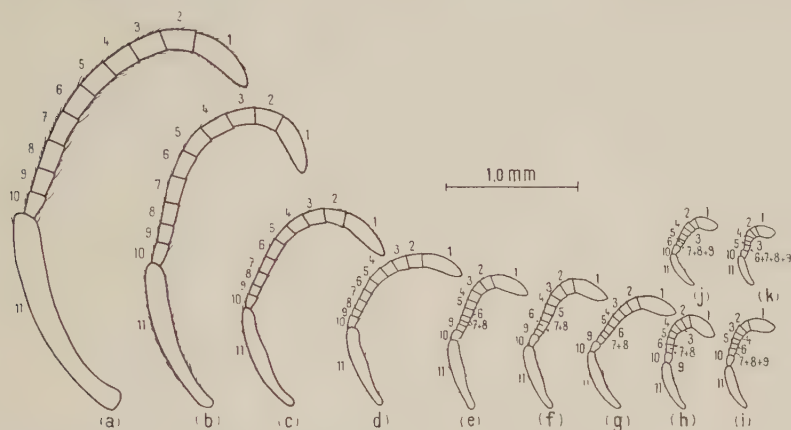


FIG. 4. — Antennae of different sized workers of *Anomma nigricans*.

(a) of the largest individual, from the 300-309 unit class; (b) from the 100-109 unit class; (c) from the 90-99 unit class; (d) from the 80-89 unit class; (e, f, g) from the 70-79 unit class; (h, i) from the 60-69 unit class; (j) from the 50-59 unit class; (k) of the smallest individual, from the 50-59 unit class.

the eighth segment is reduced in size, then partly and eventually completely undivided from the seventh segment. Such an antenna has a 9-segmented funicle. Second, the ninth segment is partly and then completely undivided from the undivided seventh and eighth segments. This funicle has eight segments. Finally, the sixth segment is partly and then completely undivided from the undivided seventh, eighth and ninth segments in the smallest individuals. The first five segments, the tenth and the scape are constant in all forms.

The reduction in the number of antennary segments of the smallest workers is a feature common to several species of army ants. Emery (1901) described a similar reduction in *Anomma wilverthi*, *Dorylus affinis*, *Dichthadia levigatus*, and *Rhogmus fimbriatus*.

The mouthparts of the major workers have been described by Cohic (1948). His description of the mandibles of the workers of different sizes is, however, neither detailed nor accurate.

The mandibles of the different sized workers are illustrated in Figure 5. They can be arranged in a continuous series. An apical and a basal tooth can be identified in all workers, though the latter is rather indistinct in

the smallest individuals. These are the only teeth present in the largest workers. Additional teeth between the apical and basal teeth become more prominent with reduction in size. One of these, the sub-apical tooth is more prominent than the others. All the teeth, other than the apical tooth, are reduced to a serrated edge in the smallest individuals. It is not possible to divide the mandibles into distinct types. There is a continuous series, with gradual modification in structure, from one extreme to the other.

The inner margins of the mandibles of workers of all sizes have long

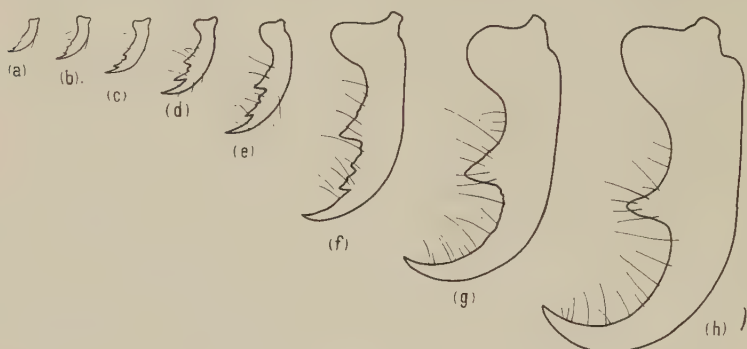


FIG. 5. — Mandibles of different sized workers of *Anomma nigricans*.

(a) of the smallest worker, from the 50-59 unit class; (b) from the 60-69 unit class; (c) from the 70-79 unit class; (d) from the 80-89 unit class; (e) from the 90-99 unit class; (f) from the 240-249 unit class; (g) of the largest individual, from the 300-309 unit class.

bristles. These are frequently broken off at their bases. They presumably have an important sensory function in these blind ants.

The large individuals defend the colony. The largest probably do little else. It is the largest individuals that come out first when a nest is disturbed. Their mandibles are extremely powerful and the apical teeth can easily pierce human skin. Frequently the tips of the apical teeth are worn down or broken through use. The smaller the mandible the more efficient as a cutting tool it would appear to be. All workers, except the very rare small individuals, have been observed to defend the colony, but their efficiency decreases with decrease in body size. The medium sized workers do the work of the colony. It is they who carry the food in a foraging expedition, or the larvae and pupae when the site of the nest is changed, while the larger individuals line the sides of the column like sentries.

The thorax.—The thorax of the workers of different sizes are similar in shape. The only clearly demarcated suture is that separating the pronotum from the rest of the thorax. There is a single large spiracle on each side above the mesothoracic legs. There is a backward-pointing spine on each side of the thorax. There is a groove ventral to this spine

covered with a number of upward-pointing bristles. Fine bristles are only found on the thorax of the medium sized individuals.

The legs of workers of different sizes are similar in structure. There is no reduction in the number of tarsal joints in the smallest individuals. The legs of the three workers illustrated in Figure 1 are shown in Figure 6.

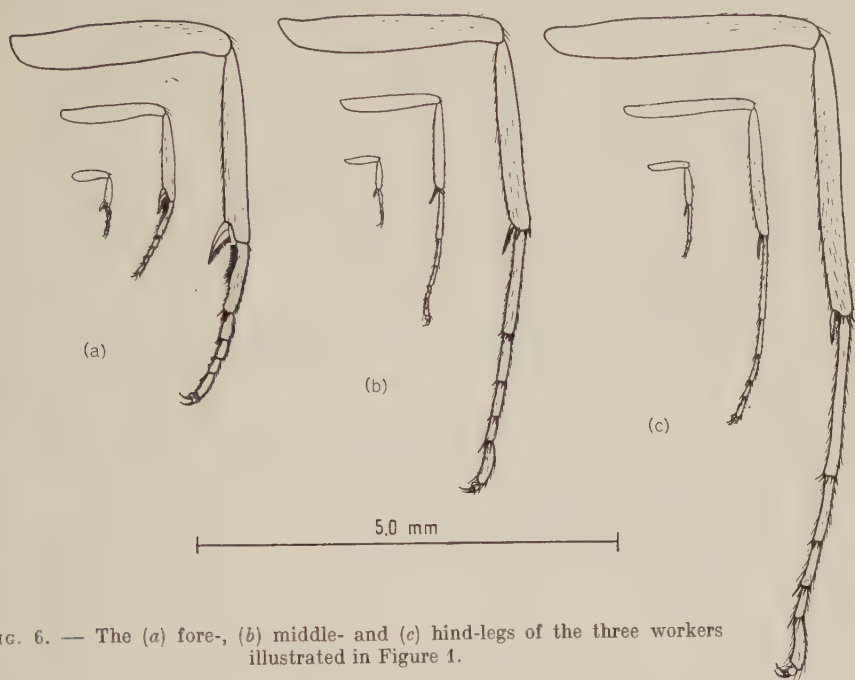


FIG. 6. — The (a) fore-, (b) middle- and (c) hind-legs of the three workers illustrated in Figure 1.

The tibial spur on the fore-legs is modified into an antenna cleaner in all workers.

The hind-leg is the longest and the fore-leg the shortest. The lengths of the fore-, middle-, and hind-legs, excluding the coxae, of the largest and smallest workers are respectively 7.0, 8.2, 11.2 mm. and 1.1, 1.2, 1.6 mm. These lengths are in the ratios of 6.4 : 6.8 : 7.0. That is, there is an increase in the relative size of the legs from the fore-legs to the hind-legs.

The petiole.—The petiole is similar in shape and structure in workers of all sizes. There is a ventral keel which bears a number of backward-pointing bristles in the larger individuals. There is a large spiracle on each side.

The gaster.—Five segments are visible in the gaster of all workers and each bears a spiracle on each side. These decrease in size from the anterior region to the posterior region. Those on the fifth segment are vestigial in the smallest individuals.

TABLE I.—THE MEAN SIZES OF THE PARTS OF THE BODY, IN ARBITRARY UNITS, AND THE PROPORTIONAL INCREASE IN THE SIZES OF THE PARTS IN DIFFERENT SIZE CLASSES.

Mid- class value.	Mandible length.		Head length.		Head width.		Thorax length.		Petiole length.		Gaster length.	
	Size.	Proport- ional increase in size.	Size.	Proport- ional increase in size.	Size.	Proport- ional increase in size.	Size.	Proport- ional increase in size.	Size.	Proport- ional increase in size.	Size.	Proport- ional increase in size.
54.5	4.9	1.00	13.7	1.00	11.7	1.00	16.1	1.00	4.6	1.00	17.0	1.00
64.5	7.3	1.49	15.8	1.45	13.8	1.18	18.0	1.12	5.2	1.13	18.5	1.09
74.5	10.0	2.04	18.0	1.34	16.0	1.37	23.0	1.43	6.0	1.30	22.0	1.29
84.5	11.1	2.27	18.3	1.34	16.2	1.39	24.6	1.53	6.3	1.37	23.6	1.51
94.5	13.0	2.65	19.6	1.43	17.6	1.50	26.9	1.67	6.9	1.50	28.0	1.65
104.5	15.1	3.08	21.7	1.58	19.9	1.70	30.5	1.89	7.8	1.70	30.4	1.79
114.5	16.4	3.35	23.3	1.70	21.4	1.83	32.8	2.04	8.4	1.83	33.1	1.95
124.5	18.1	3.69	25.3	1.85	23.6	2.02	35.4	2.20	9.2	2.00	36.1	2.12
134.5	19.8	4.04	27.9	2.04	26.1	2.23	37.9	2.35	9.8	2.13	38.5	2.27
144.5	21.4	4.37	30.6	2.23	28.4	2.43	40.6	2.52	10.6	2.30	41.3	2.43
154.5	22.6	4.61	31.4	2.29	30.2	2.58	43.8	2.72	11.2	2.44	43.4	2.55
164.5	24.8	5.06	33.8	2.47	33.3	2.85	46.0	2.86	11.8	2.57	45.5	2.68
174.5	26.9	5.49	37.4	2.73	36.6	3.13	49.6	3.08	12.6	2.74	50.4	2.97
184.5	28.7	5.86	39.5	2.88	39.3	3.36	51.6	3.21	13.8	3.00	52.0	3.06
194.5	31.0	6.33	42.2	3.08	42.2	3.61	54.6	3.39	13.8	3.00	54.3	3.19
204.5	32.0	6.53	44.1	3.22	44.5	3.80	55.2	3.43	14.9	3.24	56.6	3.33
214.5	34.4	6.94	46.0	3.36	46.6	3.98	57.8	3.59	15.2	3.30	59.8	3.52
224.5	—	—	—	—	—	—	—	—	—	—	—	—
234.5	39.3	8.02	52.7	3.85	52.7	4.50	61.0	3.79	17.3	3.76	64.7	3.81
244.5	40.0	8.16	53.0	3.87	56.0	4.79	64.5	4.01	18.0	3.91	69.5	4.09
254.5	41.0	8.37	58.5	4.27	60.5	5.17	65.0	4.04	17.0	3.70	74.0	4.35
264.5	41.0	8.37	60.0	4.38	60.0	5.13	67.0	4.16	19.0	4.13	76.0	4.47
274.5	49.0	10.00	60.0	4.38	64.0	5.47	66.0	4.10	17.0	3.70	79.0	4.65
284.5	—	—	—	—	—	—	—	—	—	—	—	—
294.5	50.0	10.20	66.0	4.82	69.0	5.90	73.0	4.53	23.0	5.00	80.0	4.71
304.5	53.0	10.82	69.0	5.04	71.0	6.07	77.0	4.78	23.0	5.00	85.0	5.00

The gaster is the most bristly part of the body. The bristles are longer ventrally than dorsally. The ventral part of the gaster is covered with fine bristles which give it a hairy appearance, particularly at the posterior end in the smaller individuals.

The genitalia of the large workers have been described by Cohic (1948).

Allometry.

Holometabolic insects are closed systems. That is, there is no increase in mass after the end of the last larval instar and consequently the size of the imago is determined by the size of the larva at pupation. Should the parts of the body of the imagines of different absolute sizes be of different proportions, the proportionally greater size of some parts will be compensated by the proportionally smaller size of other parts.

The mean lengths of the parts of the body, as measured in arbitrary units with an eyepiece micrometer, and the proportionate increase in the lengths of the parts of the workers of different absolute sizes is given in Table I.

TABLE II. — THE PROPORTION OF THE TOTAL LENGTH CONTRIBUTED BY THE DIFFERENT PARTS OF THE BODY IN INDIVIDUALS OF DIFFERENT SIZES.

MANDIBLE.	HEAD.	THORAX.	PETIOLE.	GASTER.	TOTAL LENGTH (arbitrary units).
.087	.243	.286	.082	.302	58.3
.113	.244	.278	.080	.285	64.8
.127	.228	.291	.076	.278	79.0
.129	.213	.286	.073	.298	85.9
.138	.208	.285	.073	.297	94.4
.143	.206	.289	.074	.288	105.5
.144	.204	.288	.074	.290	114.0
.146	.204	.285	.074	.291	124.1
.148	.208	.283	.073	.288	134.0
.148	.212	.281	.073	.286	144.5
.148	.206	.287	.073	.285	152.4
.153	.209	.284	.073	.281	161.9
.152	.211	.280	.071	.285	176.9
.155	.213	.278	.074	.280	185.6
.158	.216	.278	.070	.277	195.8
.158	.217	.272	.073	.279	202.8
.161	.216	.271	.071	.280	213.2
.167	.224	.260	.074	.275	235.0
.163	.216	.263	.073	.284	245.0
.160	.229	.254	.067	.290	255.5
.156	.228	.255	.072	.289	263.0
.181	.221	.244	.063	.292	271.0
.171	.226	.250	.079	.274	292.0
.173	.225	.251	.075	.277	307.0

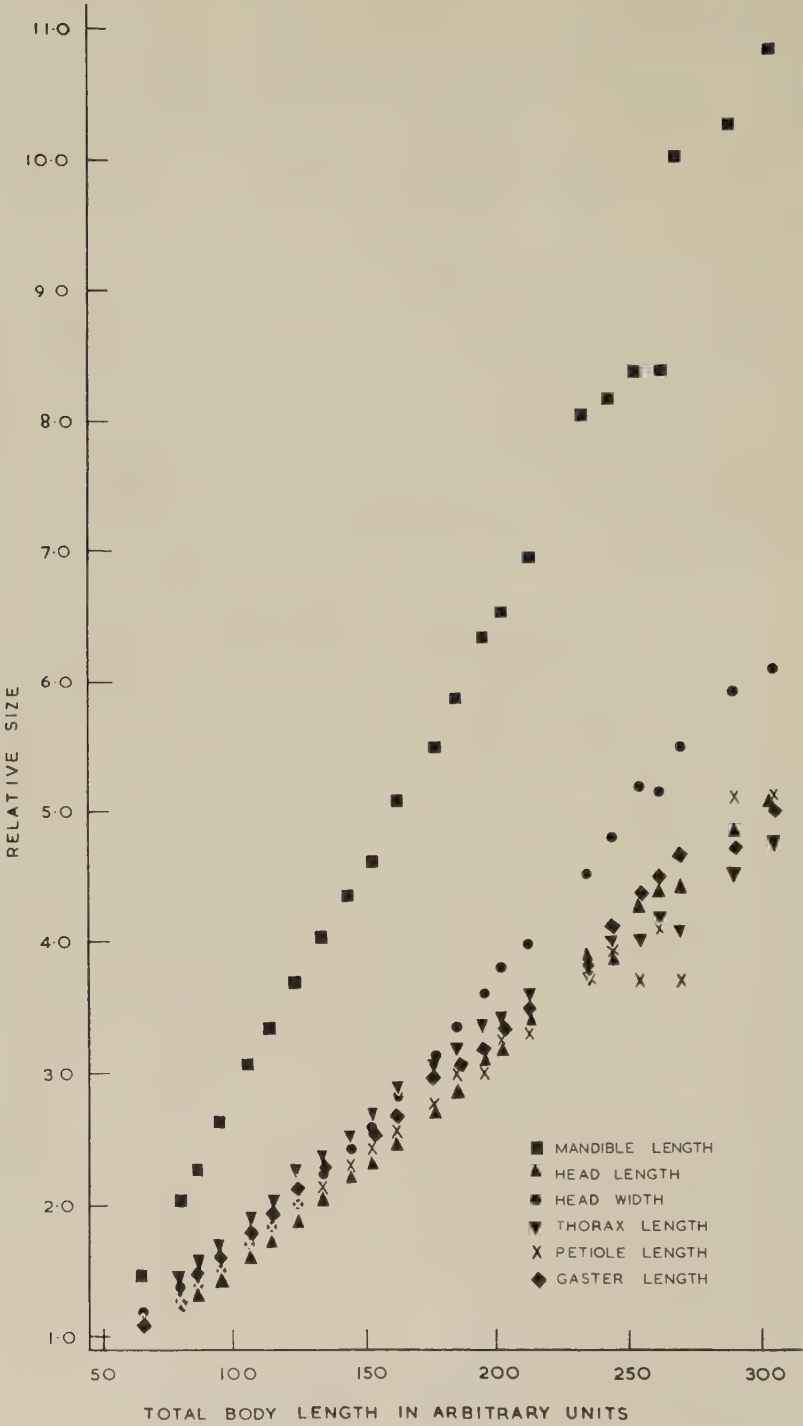


FIG. 7. — The proportional increase in the size of the parts with increase in total size.

The proportional increase in the length of the parts is plotted against mean total length in Figure 7. It is seen that the mandible is nearly eleven times as long, and the head six times as wide, in the largest workers as in the smallest. The proportional increases for the other parts are not as great.

It is seen that some parts increase in relative size and others decrease

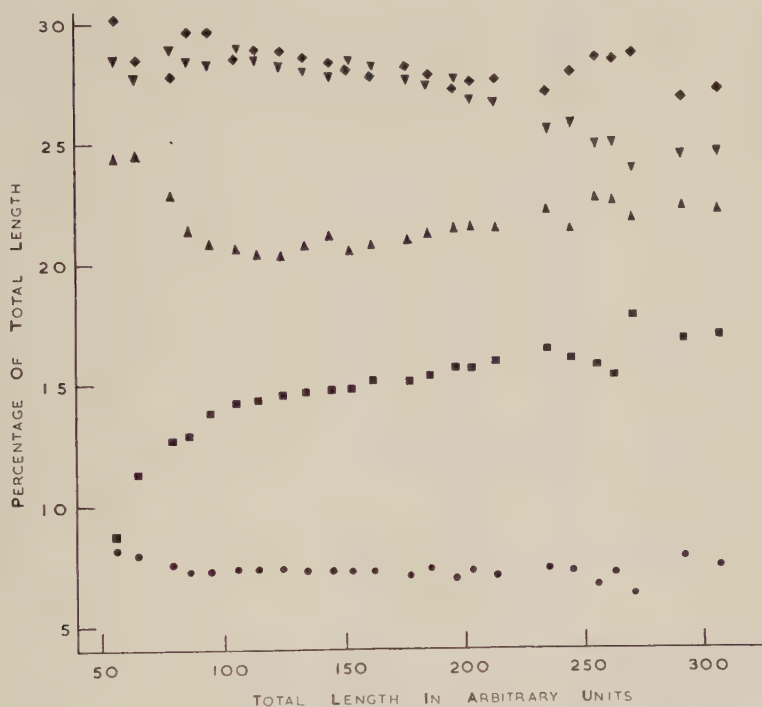


FIG. 8. — The change in the proportion of the total size contributed by the parts in different size classes. (For key to symbols, refer to Figure 7.)

in relative size when the proportions of the total length of the workers of different size classes contributed by the component parts (Table II) is plotted against the mean total class length (Fig. 8).

The mandible is the only structure that has a continual increase in relative size. The length of the head decreases in relative size in the smaller individuals, but increases in the larger individuals. The thorax decreases in relative size after a slight initial increase. The gaster decreases in relative size with increase in total size. The petiole decreases in relative size at first, but increases in relative size in the larger individuals.

Huxley (1927) and Huxley and Tessier (1936) have shown that the size of a part of the body is related to the total body size in a way which can be expressed by the general allometric formula $y = bx^\alpha$, where y is the size of the part, x is the total body size and b and α are constants, in

TABLE III. — THE LOGARITHMS OF THE MEAN SIZES OF THE PARTS OF THE BODY IN EACH OF THE SIZE CLASSES.

MID-CLASS VALUE.	MANDIBLE LENGTH.	HEAD LENGTH.	HEAD WIDTH.	THORAX LENGTH.	PETIOLE LENGTH.	GASTER LENGTH.	MEAN CLASS LENGTH.
54.5	0.069	1.137	1.068	1.207	0.663	1.23	1.751
64.5	0.863	1.199	1.14	1.255	0.716	1.267	1.812
74.5	1.0	1.255	1.204	1.362	0.778	1.342	1.898
84.5	1.045	1.263	1.21	1.391	0.799	1.408	1.934
94.5	1.114	1.292	1.246	1.43	0.839	1.447	1.975
104.5	1.179	1.337	1.299	1.484	0.892	1.483	2.023
114.5	1.215	1.367	1.33	1.516	0.924	1.52	2.067
124.5	1.258	1.403	1.373	1.479	0.964	1.588	2.094
134.5	1.297	1.446	1.417	1.579	0.991	1.586	2.127
144.5	1.33	1.486	1.453	1.609	1.025	1.616	2.153
154.5	1.354	1.497	1.48	1.642	1.049	1.638	2.186
164.5	1.395	1.529	1.522	1.663	1.072	1.658	2.209
174.5	1.43	1.573	1.564	1.696	1.1	1.702	2.248
184.5	1.458	1.597	1.594	1.713	1.14	1.716	2.269
194.5	1.491	1.625	1.625	1.736	1.14	1.735	2.292
204.5	1.505	1.644	1.648	1.742	1.173	1.753	2.307
214.5	1.537	1.663	1.668	1.762	1.182	1.777	2.239
234.5	1.594	1.722	1.722	1.785	1.238	1.811	2.371
244.5	1.602	1.724	1.748	1.81	1.255	1.842	2.389
254.5	1.613	1.767	1.782	1.813	1.23	1.869	2.407
264.5	1.613	1.778	1.778	1.826	1.279	1.881	2.42
274.5	1.69	1.778	1.806	1.82	1.23	1.898	2.433
294.5	1.699	1.82	1.839	1.863	1.362	1.903	2.465
304.5	1.724	1.839	1.851	1.887	1.362	1.929	2.487

insects whose imagines exhibit an extensive range of size. The part of the insect exhibits isometry when $\alpha = 1$. That is, its size is directly proportional to the total size. α may be greater or less than 1, in which case that part is said to be positively or negatively allometric. That is, the part is relatively greater or smaller with increase in total absolute size.

In the closed system, if some parts have a value of $\alpha > 1$, others must have a value of $\alpha < 1$ in compensation. The increase in mean total size is about 5.5 times. Only the mandible length and the head width exceed this value. We should therefore expect these parts to have the greatest values of α , which is found to be the case (Table IV).

The formula $y = bx^\alpha$ can be expressed as $\log y = \alpha \log x + \log b$. Thus any part obeying the allometric formula will fall on a straight line when the logarithm of the size of the part is plotted against the logarithm of the total size. α is the gradient of the straight line.

The logarithm of the mean length of the parts measured and of the mean total length in each size class is given in Table III and illustrated in Figure 9. Examination of the graphs suggests that all the points for each character do not fall on one straight line. Reeve and Huxley (1945) have reviewed the available data on the deviations from simple allometry.

TABLE IV.—THE EQUATIONS OF THE REGRESSION LINES ILLUSTRATED IN FIGURE 9.

MANDIBLE LENGTH

First three points	$y = 2.07223x - 2.92001$
Central fourteen points	$y = 1.19479x - 1.24837$
Last seven points	$y = 1.23710x - 1.35226$

HEAD LENGTH

First three points	$y = 0.79667x - 0.25279$
Central fourteen points	$y = 1.04299x - 0.76993$
Last seven points	$y = 1.05060x - 0.77354$

HEAD WIDTH

First three points	$y = 0.91230x - 0.52284$
Central fourteen points	$y = 1.19386x - 1.11620$
Last seven points	$y = 1.12004x - 0.92628$

THORAX LENGTH

First three points	$y = 1.06509x - 0.66370$
Central fourteen points	$y = 0.94475x - 0.43019$
Last seven points	$y = 0.81746x - 0.15155$

PETIOLE LENGTH

First three points	$y = 0.78046x - 0.70142$
Central fourteen points	$y = 0.97306x - 1.07838$
Last seven points	$y = 1.19147x - 1.60983$

GASTER LENGTH

First three points	$y = 0.76874x - 0.11910$
Central fourteen points	$y = 0.92846x - 0.38895$
Last seven points	$y = 0.93353x - 0.38790$

They found that variations in the growth rate in organisms of different sizes occur commonly in the vertebrates and in holometabolic insects. They point out that it is not usually possible to test whether the allometry is curvilinear or consists of two or more straight lines in these cases. There is no justification, other than that of convenience, for fitting more than one straight line instead of a single curve to the data in such cases.

The central 14 points appear to fall on a straight line in the present case. The first three and the last seven appear to fall on lines whose gradients differ from those formed by the central 14 points. The equations of these lines have been calculated. They are given in Table IV and illustrated in Figure 9.

It is found that, apart from the gaster, the gradients of the three lines for the six regions of the body measured are significantly different (Table V).

The mandible has a positive allometry in all sizes of individuals. It is very high in the smallest individuals, and higher in the larger than in the medium sized individuals. This confirms the conclusions drawn from Figure 8. The head length has a negative allometry in the smaller individuals, but has an increasingly positive allometry with increase in

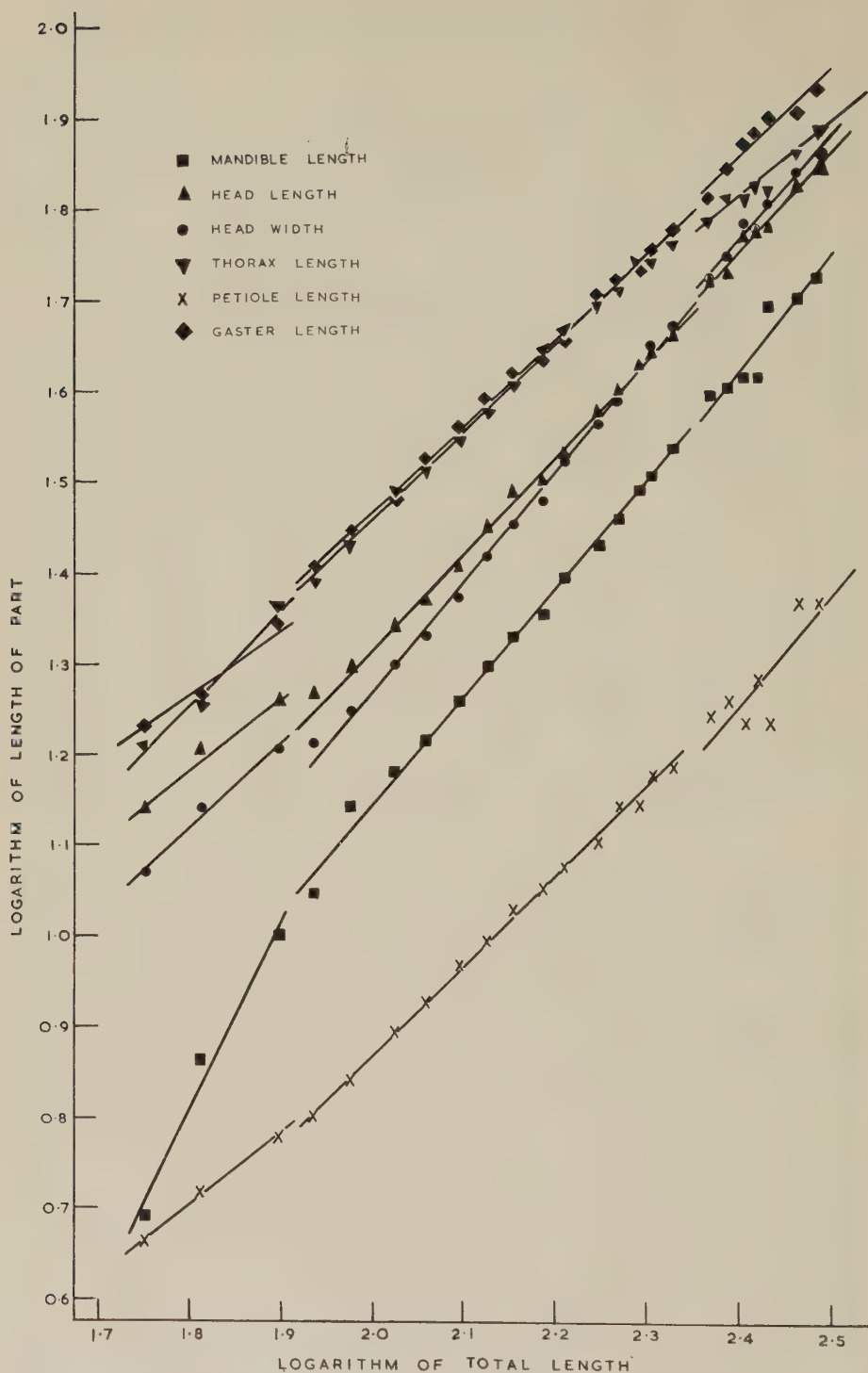


FIG. 9. — The allometry of the parts of the body in different size classes together with regression lines fitted to the data.

TABLE V.—THE ALLOMETRIC CONSTANTS FOR THE DIFFERENT PARTS OF THE BODY IN SMALL, MEDIUM AND LARGE INDIVIDUALS.

		FIRST THREE POINTS.	CENTRAL FOURTEEN POINTS.	LAST SEVEN POINTS.
MANDIBLE LENGTH	α	2.07223	1.19479	1.23710
	t	94.98	11.526	
	d.f.	13	17	
	p	< .001	< .001	
HEAD LENGTH	α	0.79667	1.04299	1.0506
	t	37.326	3.052	
	d.f.	13	17	
	p	< .001	.01 > p > .001	
HEAD WIDTH	α	0.9123	1.19386	1.12004
	t	42.696	26.524	
	d.f.	13	17	
	p	< .001	< .001	
THORAX LENGTH	α	1.06509	0.094475	0.81746
	t	27.652	72.339	
	d.f.	13	17	
	p	< .001	< .001	
PETIOLE LENGTH	α	0.78046	0.97306	1.19147
	t	38.186	38.304	
	d.f.	13	17	
	p	< .001	< .001	
GASTER LENGTH	α	0.76874	0.92846	0.93353
	t	50.865	2.416	
	d.f.	13	17	
	p	< .001	.02 > p > .05	

absolute size. The head width is negatively allometric in the smaller individuals, but has a highly positive allometry in the medium sized individuals and a surprisingly less positively allometry in the larger individuals.

Huxley (1932) explained the diminished allometry of the head width in the larger workers of *Anomma nigricans* as being the result of competition between the incompletely developed organs with high growth ratios and the rest of the body for the limited reserves of food materials in the pupa. The reduction in the value of α for the head width in the largest individuals is in compensation for the increased value of α for the mandible, head length and petiole. The growth rates are not constant for all the developing structures in different sized individuals. For example, the mandible has a very high value of α in the smaller individuals, this high value being compensated by the low value of α for the head. The growth processes are concentrated on producing a mandible at the expense of a head in the small individuals.

The smallest individuals are probably abnormally small. Not only are the mandibles below the expected size, but the antennae have less than the normal number of segments. They probably arise as the result of pupation at an early instar, this being due to irregular and underfeeding by their nurses.

The positive allometry of the anterior region of the body is compensated by the negative allometry of the posterior region in the larger individuals. This is illustrated in Table VI.

TABLE VI.—THE DISTRIBUTION OF POSITIVELY AND NEGATIVELY ALLOMETRIC STRUCTURES IN INDIVIDUALS OF DIFFERENT SIZES.

	SMALL INDIVIDUALS.	MEDIUM INDIVIDUALS.	LARGE INDIVIDUALS.
MANDIBLE LENGTH.	++++	++	+++
HEAD LENGTH.	---	+	++
HEAD WIDTH.	—	++	+
THORAX LENGTH.	+	—	—
PETIOLE LENGTH.	---	—	+
GASTER LENGTH.	---	—	—

The growth processes are complex and are not constant in all sizes of individuals. The primary "growth centre" (Huxley, 1932) is in the mandibles in the smallest individuals. It spreads to the head with increase in absolute size. There is evidence of a secondary growth centre in the thorax of smaller individuals, but this disappears with increase in absolute size. There is also a secondary growth centre in the petiole of the larger individuals.

Polymorphism.

The lengths of a sample of the ants collected are given in the size frequency distribution in Figure 10 A. This distribution is positively skewed, with a mode at the 110-119 unit class. The smallest individuals in the sample belong to the 60-69 unit class and the largest to the 290-299 unit class. Both smaller and larger individuals were found when all the ants collected were examined. The smallest individual was 53 units long and the largest 307 units long. These extremes are very rare.

The tail of the distribution is long and irregular. There is a possible second mode at the 190-199 unit class. The lengths of the ants were replotted on a logarithmic scale in order to eliminate the irregularities. This is shown in Figure 10 B. The frequency distribution now resembles two overlapping normal frequency distributions. A normal curve was fitted to the data from the first fifteen classes and another to the data from

the last eight classes. These curves are shown superimposed over the histograms. These curves, however, are found not to be good fits to the data. There is a large contribution to χ^2 by the fifth, sixteenth and seventeenth classes. Thus the analysis does not agree with the hypothesis that the data represents two overlapping normal distributions. It is possible that a larger sample would have given a better fit. However, the existence of bimodality is not invalidated, but has been emphasised by the plotting of the lengths on a logarithmic scale.

Bimodality is not uncommon in the size frequency distribution of worker ants (Wilson, 1953 and 1954). It is associated with the division of labour into functional castes, but while the distribution is continuous there can be no complete division of labour. It is well established that the evolution of castes in ants has been towards the establishment of two distinct worker forms, large aggressive individuals (majors or soldiers) whose function is to defend the colony and to do special tasks, and smaller individuals (minors or workers proper) whose function is to tend the brood and to collect food. Evolution has led towards the elimination of the intermediate sized individuals (medias). The army ants have not reached this last stage.

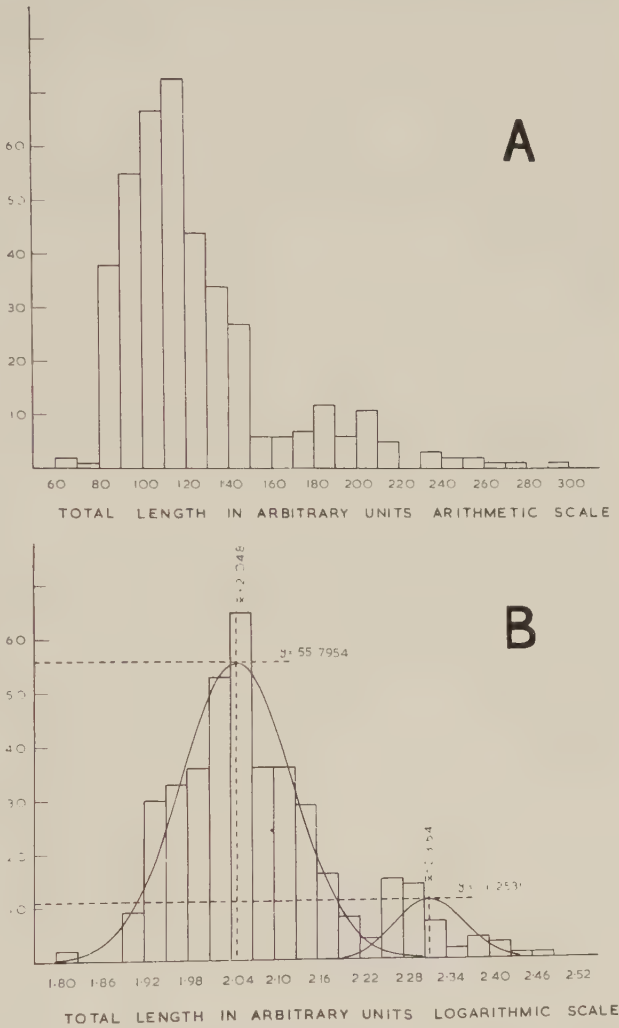


FIG. 10. — The size frequency distribution of a sample of workers of *Anomma nigricans*.
A. Arithmetical scale. B. Logarithmic scale.

It is therefore strange that Cohic (1948) should have endeavoured to demonstrate the existence of not two, but four distinct morphological types among the workers in his study of *Anomma nigricans*. Cohic measured some 800 individuals which he arranged in 61 classes. That is, there was one class for each unit of measurement and therefore no grouping. He claimed to have obtained a quadrimodal distribution, each mode of which corresponded to a different morphological type.

The first type, consisting of the smallest individuals, is characterised by the head being longer than wide, wider behind than in front, with a large prominent clypeus and mandibles with multiple serrations, but no prominent teeth. That is, individuals like Figures 2 (f) and 5 (a)-(c). He claimed that 43.4 percent of the individuals were like these. He called them the workers.

The second, third and fourth types were described as the micro-, meso-, and macrocephalic soldiers, which constituted 46.7 percent, 8.2 percent and 1.6 percent of the individuals respectively. The microcephalic soldiers are described as having a prominent clypeus and a head longer than wide. They differ from the workers in having a head wider in front than behind and in having mandibles with two distinct equal sized sub-apical teeth. That is, individuals like Figures 2 (c), and 5 (d)-(e). The mesocephalic soldiers are described as having a reduced clypeus and a head as wide as it is long, and wider in front than behind. The mandible has a large basal and apical tooth and the sub-apical teeth relatively smaller. That is, individuals like Figures 2 (b) and 5 (f). The macrocephalic soldiers are described as having an extremely reduced clypeus and a head wider than long. The mandible is falciform and with only the apical and basal teeth present. That is, individuals like Figures 2 (a) and 5 (h).

Such a classification is fanciful as it bears no relation to reality. The workers cannot be divided into these distinct classes and the frequency distribution is not quadrimodal. Cohic's misinterpretation of the polymorphism is largely due to the qualitative differences in the mandibles of different sizes. Huxley (1932) has shown in Lucanid beetles how allometry affects mandible structure. The army ants are just like Lucanid beetles in this respect. There is a continuous morphological sequence from one extreme to the other. The most abundant workers are those like Figures 1 (b), 2 (c) and 5 (f). The smallest individuals are very rare and do not constitute even 1 percent of the total. I regard them as subnormal individuals resulting from extreme premature pupation. Cohic supported his claim for four distinct classes of workers with allometric studies. But it must be assumed that he has interpreted his results to fit a preconceived theory as it is not clear how he obtained his allometric coefficients.

There are two schools of thought on the origin of the female castes. There are those who believe that the differences between the different female castes are genetically determined and those who believe they are due to environmental causes alone. The greatest exponent of the first theory was W. M. Wheeler. He believed that because the female castes

were so highly adaptive they must have a genetic determination, although he admitted that underfeeding caused premature pupation and therefore smaller imagines. All that the environment furnished were the conditions for the attainment of the characters predetermined by heredity. He postulated that the worker characters were transmitted to the next generation by the haploid males produced by the workers when they mated to normal diploid females. There is no experimental evidence in support of this theory.

Huxley (1927, 1932) was the first to point out that a genetic explanation was not necessary. He argued that underfeeding of the larvae by their nurses combined with the ability of these larvae to pupate prematurely will produce an allometric series of imagines. This theory has been extended in a review of ant polymorphism by Wilson (1953). Wilson (1954) concluded that all stages from simple monomorphism to complete dimorphism are explicable on the allometry produced by the variable feeding of the larvae combined with the progressive divergence of two larval types. Wilson supposed five stages:

1. *Monophasic isometry*—in which all the workers are of equal size and do not exhibit allometry.

2. *Monophasic allometry*—in which the workers are variable in size and in which the extremes are functional castes.

3. *Diphasic allometry*—in which the workers have a bimodal frequency distribution. The workers of the two modes, which are functional types, have different allometric constants.

4. *Triphasic allometry*—in which the smallest workers (minors) and the largest workers (majors or soldiers) are separated by a rare intermediate group (medias), the three types having different allometric constants.

5. *Complete dimorphism*—in which the workers are of two distinct types (minors and majors) due to the elimination of the medias.

Anomma nigricans belongs to group 3 on this classification. The lower values of α correspond, however, not to the minors but to the abnormally small individuals. It is not possible to detect a separate value of α for the individuals intermediate between the two modal groups.

Summary.

The object of the paper is to dispute the contention of Cohir (1948) that the workers of *Anomma nigricans* exist as four distinct morphological types.

It is found that there is a continuous morphological series of workers from the smallest to the largest, the largest being about 75 times the volume of the smallest. There is a considerable change in shape with change in size. This is particularly noticeable in the head. The structure of the head capsule, mandibles and antennae are described in detail.

Measurements of the parts of the body of different sized workers shows

that the different parts of the body are in different proportions in different sized individuals. That is, some parts increase in relative size while others have a compensatory decrease. This is because all the parts of the adult insect have to compete for the limited amount of food material available in the pupa. There is a primary "growth centre" (Huxley, 1932) in the mandible.

It is found that the allometry is not simple because the various parts of the body have different allometric constants in different sized individuals. Three straight lines are fitted to the data instead of a single curve for convenience only. The size frequency distribution resembles two overlapping normal distributions when plotted logarithmically.

It is concluded that the workers of *Anomma nigricans* exhibit diphasic allometry (Wilson, 1953) and that Cohic's contention is disproved.

Résumé.

Le but de l'article est de contester l'affirmation de COHIC (1948), à savoir qu'il existe quatre types morphologiques distincts d'ouvrières d'*Anomma nigricans*.

On constate qu'il y a une série morphologique continue d'ouvrières de la plus petite à la plus grande, le volume de la plus grande étant environ 75 fois plus grand que celui de la plus petite. Il y a un changement très sensible dans la forme lorsque la taille change. Ceci est particulièrement apparent dans la tête. La structure de la capsule céphalique, les mandibules et les antennes sont décrites en détail.

Les mensurations des parties du corps d'ouvrières de taille différente indiquent que les différentes parties du corps sont en proportions différentes chez des individus de taille différente. Ce qui revient à dire que, par rapport à d'autres, certaines parties croissent en taille, tandis que d'autres décroissent d'une façon compensatrice. Ceci se produit car toutes les parties de l'insecte adulte doivent lutter pour la quantité limitée de nourriture disponible dans la nymphe. Il y a un « centre de croissance » primaire (HUXLEY, 1932) dans la mandibule.

On constate que l'allométrie n'est pas simple, car les différentes parties du corps ont des constantes allométriques différentes chez des individus de taille différente. Trois lignes droites sont indiquées sur les données au lieu d'une seule courbe pour convenance seulement. La distribution de fréquence de la taille est semblable à deux distributions normales imbriquantes lorsqu'elles sont tracées en coordonnées logarithmiques.

On en conclut que les ouvrières d'*Anomma nigricans* présentent une allométrie diphasée (WILSON, 1953) et que l'affirmation de COHIC est réfutée.

Резюме

Цель этой работы оспорить утверждение Соhic (1948), что работники *Anomma nigricans* существуют как четыре отдельных морфологических типа.

Установлено, что существует постоянная морфологическая серия работников от самых малых до самых больших, при чем последние в 75 раз больше по объему, чем первые. С изменением величины изменяется и форма. Это особенно заметно в голове. Строение головной капсулы, мандибула и антенны подробно описано.

Из размеров частей тела работников, отличающихся друг от друга своей величиной, можно видеть, что разные части тела индивидуумов разной величины имеют разные соотношения, т.е. некоторые части увеличиваются в смысле относительных размеров, в то время как другие части компенсирующе уменьшаются. Это происходит вследствие того, что все части взрослого насекомого должны состояться за ограниченное количество пищи, имеющейся в куколке. В мандибуле имеется основной "центр роста" (Huxley, 1932).

Установлено, что аллометрия здесь не простая потому, что разные части тела индивидуумов разной величины имеют разные аллометрические постоянные. Для удобства только к данным применены три прямые линии вместо одной кривой. Распределение размерной частоты похоже на два перекрытых нормальных распределения, если их построить логарифмически.

Выводится заключение, что работники *Anomma nigricans* проявляют дифазную аллометрию (Wilson, 1953), и что утверждение Кюгича опровергнуто.

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OBSERVATIONS ON THE BEHAVIOR OF *BOMBUS DIVERSUS* SMITH (BIOLOGICAL STUDIES ON JAPANESE BEES, XIII)

by Setsu MIYAMOTO

(Laboratory of Entomology, Hyogo University of Agriculture, Sasayama, Hyogo, Japan.)

Bombus (Diversobombus) diversus Smith is a common species in Sasayama basin, Hyogo Pref., Japan. This bumblebee is one of the most dominant visitors for tubular flowers, due to its well-developed or elongated tongue to A-group*¹. On the biology of this species has been only publication (Morimoto, Iwata and Yasumatsu, 1951). The biological studies on our bumblebees make just a start in our country. As the first step of the study, it ought to obtain the knowledge on their life or activity in the field.

This paper deals with the behavior or activity of workers in 3 colonies of early, middle, and developed or ending stage during June to November of 1958, in comparison with that of *Bombus (Pratobombus) ardens* Smith already published by the writer (Taniguchi 1955, Miyamoto 1957 a, b). Furthermore, some brief account of the general characters of males, workers, new and old females of *diversus* are also added here from the field data since 1952.

The writer wishes to express her thanks to Prof. K. Iwata of the Hyogo University of Agriculture for his constant guidance and suggestions and for reading this manuscript. I am also indebted to Dr. S. F. Sakagami of the Hokkaido University for his kind criticism and aid in many ways, and thanks are also due to Mr. T. Nakane of the Kyoto Prefectural University for the identification of *Antherophagus nigricornis* Fabricius.

1^o — Outline of the life.

The nesting life of this species is continued during from spring to autumn. In general, the queen appears late in April, the workers in middle of May, and males and new females in September-October. Their life ends early or middle November.

Appearance of females after hibernation—The appearance of females from winter-quarters and search of the nesting site were observed during the period from middle or late April to late May. The field notes on females in spring of 1953-1957 are summarized in Table 1. There were also added some results of dissection of digestive and reproductive organs. From the Table, following knowledge may be obtained. 1. The individual-

*¹ The bee species belonging to A-group (the ratio of median glossa length to head width is 2.5-3.4) among 51 species of Apoidea examined by the writer (Taniguchi 1954), were 5 species of *B (Diversobom.) diversus* Smith, *B (Hortobom.) tersatus* Smith, *B (Agrobom.) senilis* Smith, *Anthophora acervolum villosula* Smith and *Anthophora florea* Smith.

ity is in both times of appearance and nest foundation of females after hibernation. 2. The appearing females visit flowers for sucking nectar or eating pollen for the first time. 3. The ovaries of females were quite immature at the appearing time. This pollinomeliphagous habit may be continued till the time of maturation of ovaries. And then, probably, they start searching for nest sites*2.

TABLE I. — ACTIVITIES AFIELD OF FOUNDING FEMALES JUST AFTER HIBERNATION.

DATE.		FLOWER SPECIES VISITED BY FOUNDING FEMALES OR THEIR BEHAVIOR WHEN SEARCHING FOR NESTING SITES.
1953	15.V 26.V	<i>Lamium album</i> L. var. <i>barbatum</i> Franch. et Sav. (for nectar). <i>Abelia serrata</i> Sieb. et Zucc. (for nectar).
1954	24.IV	<i>Lamium album</i> L. var. <i>barbatum</i> Franch et Sav. (for pollen).
1955	27.IV 21.V 21.V 24.V 30.V 1.VI	*1 <i>Brassica campestris</i> L. subsp. <i>Rapa</i> Hook. fil. et Anders (for nectar). <i>Lamium album</i> L. var. <i>barbatum</i> Franch. et Sav. (for pollen). *2 <i>Weigela hortensis</i> C. A. Mey. forma <i>spontanea</i> Makino (for nectar). *3Flying for nesting site in sunny bank. <i>Weigela coræensis</i> Thunb. (for pollen). <i>Styrax japonica</i> Sieb. et Zucc. (for nectar).
1956	17.IV 26.IV 26.IV 4.V 12.V 12.V 28.V	Flying for nesting site above ground surface piled up with dead leaves in <i>cryptomeria</i> wood. <i>Elæagnus multiflora</i> Thunb. (for nectar). <i>Rhododendron</i> sp. (for nectar). Flying for nesting site above ground surface in sunny slope of a bank. <i>Rhododendron dilatatum</i> Miq. (for nectar). <i>Monotropastrum globosum</i> H. Anders (for nectar and pollen*4). Flying for nesting site, above ground surface of a bank covered with pine needle and often crawling to investigate likely spots.
1957	6.V 9.V 10.V	<i>Epimedium macranthum</i> Morr. et Decne. var. <i>violaceum</i> France (for nectar and pollen*4). <i>Epimedium macranthum</i> Morr. et Decne. var. <i>violaceum</i> France (for nectar). Flying for nesting site in sunny slope.
		*1 Results of dissection: nectar existed in nectar stomach (NS), pollen was detected in digestive organ (PE), and ovary had no oocyte visible by binocular. *2 Results of dissection: NS, PE and ovary had half grown eggs (Degree of development of oocytes was indicated by 1 [mature oocytes], 2/3, 1/2 and 1/3). *3 Results of dissection: NS and ovary had 1, 1', 2/3 and 1/2 sized oocytes. *4 With large-sized pollen mass in basket.

Appearance of the first workers and their flower visiting—Small sized workers*3 firstly produced by the founding females appeared on May.

*2 The different cases from this supposition were observed by Sakagami. But, he wrote to me that this supposition was adaptable in the main.

*3 The criterion in body-size of foragers indicated as small, medium and large are approximately as follows. Small: head width < 3.0 mm, wing length: < 8.3 medium: h.w. < 3.5, w.l. < 10.4, large: h.w. < 4.0, w.l. < 13.0.

The first observation on their flower visiting in 1952-1957 are as follows: 14.V.1952 (*Rhododendron* sp.), 15.V.1953 (*Rubus morifolius* Sieb., *Rubus palmatus* Thunb.), 29.V.1954 (*Rosa multiflora* Thunb.), 13.V.1955 (*Vicia unijuga* Al.Br.), 28.IV.1956 (*Prunella vulgaris* L., *Cirsium japonicum* D.C., *Melampyrum roosum* Maxim. var. *japonicum*) and 23.IV.1957 (*Astragalus sinicus* L.). The number of flower species visited by these workers during 6 months from May to October were 12 species (May) → 29 species (June) → 29 species (July) → 6 species (August) → 15 species (September) → 12 species (October) as indicated in detail in the Table 2*4.

New females—The emergens of new females was observed at nest C (observation nest in 1958). In 30 min. (10:30-11:00) of October 27, 3 new females departed with careful orientation flights, and 2 of them returned from their first trip probably for nectar to nourish themselves. Up to November 8, their trips for nectar were observed. Sometimes, some new females crawled out from the nest, but was unable to take wing and turned back quickly to enter nest.

Male bees—I have poor data on the male bees. The flowers visited by males were *Cirsium spicatum* Matsum. (20.IX.1954) and *Impatiens textori* Miq. (1.X.1955). In nest C, no data were obtained on the appearance of male bees although the emergence of new females were observed. It seems that the time of departing nest in male bees is limited in early morning similarly in the case of male *ardens**5.

2° — Observation nests.

Nest A—Discovered in the tall hedge of bamboo on south slope of a reservoir bank on June 20, 1958. In an hour of my first observation from 10:40 to 11:40 of June 21, 8 workers went out and 9 returned. Seven of workers returned with pollen loads. All of them were of medium-size and of fresh bodies. On this nest, 3 all-day and some fragmental observations were carried out.

Nest B—Discovered 10 meters apart from nest A on July 18, 1958. The nest entrance was 3 cm. in diameter and was situated on a ridge surrounded by rice fields. Three all-day and some fragmental observations were made.

Nest C—This prosperous nest discovered by Dr. K. Iwata was situated on a bank of hemp palm thicket facing west on October 9, 1958. In 30 min. of my first encounter from 16:15 to 16:45 on that day, 20 workers went out and 22 returned. A all-day and many fragmental observations (2 or 3 times daily) were made during a month from October 9 to November 8. As results of observations data were obtained relating to activity

*4 This variation of the number of flower species visited by the bee corresponds roughly to the seasonal shift of the number of flowering plant species in Sasayama.

*5 *Bombus (Pratobombus) ardens* Smith appears only from beginning of spring to the beginning of summer in Sasayama. The queen appears early in April, the workers in May, and males and new females in June. Their nesting life ends early in July (Taniguchi [= Miyamoto], 1955).

TABLE II.—KINDS OF FLOWERS VISITED BY WORKERS OF *Bombus diversus*
IN SASAYAMA BASIN.

April

Prunella vulgaris L.
Cirsium japonicum D.C.
Melampyrum roseum Maxim. var. *japonicum* Maxim.

May

Rosa multiflora Thunb.
Rubus morifolius Sieb.
Rubus palmatus Thunb.
Rhododendron sp.
Rhododendron linearifolium Sieb. et Zucc., var. *macrosepalum* Makino.
Astragalus sinicus L.
Trifolium pratense L.
Trifolium repens L.
Vicia unijuga Al.Br.
Weigela coraeensis Thunb.
Weigela hortensis C.A.Mey. forma *sponsanea* Makino.
Lamium album L., var. *barbatum* Franch et Sav.

June

Vicia unijuga Al.Br.
Trifolium repens L.
Trifolium pratense L.
Sophora angustifolia Sieb. et Zucc.
Rhaseolus vulgaris L.
Dolichos lablab L.
Astragalus sinicus L.
Vicia sativa L.
Styrax japonica Sieb. et Zucc.
Nandiana domestica Thunb.
Callicarpa japonica Thunb.
Ligustrum ibota Sieb. var. *angustifolium* Blume.
Campanula punctata Lan.
Citrus Junos Tanaka
Viola sp.
Castanea pubinervis Schneid.
Prunella vulgaris L.
Rhododendron sp.
Hosta undulata Bailey var. *errromena* F. Maekawa.
Hosta sieboldiana Engl.
Antirrhinum majus L.
Diospyros Kaki L. fil.
Rubus parvifolius L.
Rosa multiflora Thunb.
Weigela coraeensis Thunb.
Lonicera japonica Thunb.
Deutzia crenata Sieb et Zucc.
Cirsium japonicum D.C.

July

Cirsium japonicum D.C.
Vicia unijuga Al.Br.
Sophora angustifolia Sieb et Zucc.
Trifolium pratense L.
Trifolium repens L.
Dolichos lablab L.
Caesalpinia sepiaria Roxb. var. *japonica* Makino
Indigofera pseudo-tinctoria Matsum.
Lotus corniculatus L. var. *japonicus* Regel.
Vi na catiang Endl., var. *sininsis* King.

Nandiana domestica Thunb.
Salvia japonica Thunb.
Scutellaria indica L.
Prunella vulgaris L.
Hosta undulata Bailey var. *errromena* F. Maekawa.
Hosta sieboldiana Engl.
Polygonatum falcatum A. Gray.
Stellaria media Cyr.
Dianthus superbus L.
Campanula punctata Lan.
Lysimachia clethroides Duby
Cucumis satinus L.
Cucurbita mischata Duch. var. *melonaeformis* Makino.
Solanum melongena L. var. *esculentum* Ness.
Ilex crenata Thunb.
Impatiens Balsamina L.
Impatiens textori Miq.
Styrax japonica Sieb. et Zucc.
Callicarpa japonica Thunb.
Mallotus japonicus Muell. Arg.

August

Cucurbita mischata Duch. var. *melonaeformis* Makino.
Ipomoea Nil Roth.
Lychnis migueliana Rohab.
Lespedeza bicolor Turcz., var. *japonica* Nakai.
Vicia unijuga Al.Br.
Impatiens Balsamina L.

September

Elaeagnus multiflora Thunb.
Crawfurdia japonica Sieb. et Zucc.
Aconitum chinensis Sieb.
Rubus hakonensis Franch. et Sav.
Liriope graminifolia Baker
Tricyrtis birta Hook.
Caryopteris divaricata Maxim.
Callicarpa japonica Thunb.
Pertya ovata Maxim.
Mosia punctata Maxim.
Salvia chinensis Benth.
Lespedeza bicolor Turcz. var. *japonica* Nakai.
Vicia unijuga Al.Br.
Dunbaria villosa Makino.
Impatiens textori Miq.

October

Plectranthus inflexus Vahl.
Plectranthus longitubus Miq.
Salvia chinensis Benth
Impatiens textori Miq.
Polygonum sagittatum L. var. *siebold* Maxim.
Polygonum flaccidum Meisn.
Cucurbita mischata Duch. var. *melonaeformis* Makino
Gentiana scabra Bunge. var. *Buergeri* Maxim.
Pertya ovata Maxim.
Cirsium Hilgendorfi Makino.
Cosmos bipinnatus Cav.
Solidago Virga-aurea L.

TABLE III.—NUMBER OF DEPARTING (D) OR RETURNING (R) FORAGERS OF 3 NESTS IN EVERY 30 MIN. OF 7 ALL-DAY OBSERVATIONS DURING JUNE TO OCTOBER.

NESTS.	A				A				A				B				B				B				C			
	27.VI.1958				4.VII.1958				18.VII.1958				25.VII.1958				22.VIII.1958				29.VIII.1958				17.X.1958			
	D	R	P*		D	R	P		D	R	P		D	R	P		D	R	P		D	R	P		D	R	P	
7:00-7:30	8	14	13		18	26 ^a	2		24	20	7		4	9	9		5	6	2		14	14			14	14	8	
7:30-8:00	4	9	8		13	17	1		20	18	7		4	6	6		3	2	1		24	22			24	22	14	
8:00-8:30	7	7	6		4	12	0		13	18	6		9	6	6		6	2	4		6	17			6	17	8	
8:30-9:00	2	5	4		11	19	1		15	19	6		4	4	9		4	6	4		23	24			23	24	44	
9:00-9:30	4	3	2		11	19	1		5	5	4		5	4	5		4	0	1		0	1			0	1	15	
9:30-10:00	4	6	3		13	11	0		3	11	8		4	4	5		5	5	3		5	3			5	3	15	
10:00-10:30	3	4	1		10	16	2		4	12	3		3	3	4		2	6	2		25	17			25	17	10	
10:30-11:00	3	4	2		18	14	2		4	8	3		2	2	2		3	3	4		28	30			28	30	16	
11:00-11:30	0	2	0		18	15	7		4	5	3		2	4	4		2	3	2		21	19			21	19	14	
11:30-12:00	1	0	0		15	15	7						1	2	2		2	4	1		20	24			20	24	16	
12:00-13:00	3	5	2		14	14	7		5	4	0		4	3	2		2	5	4		27	25			27	25	18	
13:00-13:30	3	5	2		11	14	10		4	4	3		4	3	2		2	4	2		18	25			18	25	16	
13:30-14:00	7	5	1		10	13	9		8	7	2		2	4	4		2	4	2		4	3			4	3	18	
14:00-14:30	3	7	2		11	10	7		9	8	3		3	5	3		2	3	1		7	25			7	25	16	
14:30-15:00	6	7	2		11	10	7		10	10	4		5	5	5		3	6	4		20	24			20	24	16	
15:00-15:30	13	8	2		4	11	8		16	10	3		3	3	2		2	7	1		4	1			4	1	21	
15:30-16:00	17	11	2		16	7	4		14	12	5		6	3	4		4	9	5		28	30			28	30	19	
16:00-16:30	10	14	7		10	9	5		15	15	6		8	5	5		5	12	7		23	23			23	23	22	
16:30-17:00	13	11	5		14	16	8		19	15	7		16	7	8		7	7	3		25	32			25	32	21	
17:00-17:30	16	16	5		12	12	2		22	18	8		22	8	8		8	7	3		14	21			14	21	15	
17:30-18:00	15	15	4		16	17	9		24	22	6		24	10	8		8	6	5		1	25			1	25	12	

of workers, emergence of new females and disappear of foragers or workers in the latter half of *diversus* colony life up to its collapse.

3° — Foraging trips in the daytime.

In Table 3, are shown the number of departing or returning foragers in every 30 min. of 7 all-day observations in 3 nests during from June to October. In Fig. 1, are plotted the number of trips and temperatures in every 30 min. of 3 all-day*⁶ observations in 3 nests. The curves plotted by the number of foraging trips in every 30 min. of a day are a V-shaped in the period during from June 27 to August 29. The curve seems to be a typical curve as well as that of trip density*⁷ in the case of *ardens*, as reported previously (Miyamoto, 1957 *a, b*). Such curve is due to increase of foraging trips in the morning and evening, and decrease in midday (11:00-14:00). But a different type of curve is indicated by trip density in nest C, which is very irregular.

Except the case in nest C (October 17), a converse correlation is found between the curves of trip density and day-long temperature. In those observation days, the temperature was properly low in the morning and evening and considerably high in midday. In summer, the number of trips indicates the minimum value and temperature show the maximum in midday.

In autumn, the curve of trip density runs in about parallel with the curve of temperature through the daytime, that is, the rising temperature is accompanied by the increase of number of trips.

The V-shaped curve in summer seems to be due to high temperature in midday, which weaken the foraging activity of those bees. In autumn, on the other hand, the increasing of number of trips goes together with rising temperature. No other seasonal variations were recognized as for their foraging activities during June to October.

4° — Variation of number of foraging trips.

In order to know the seasonal variation of foraging activity or to ascertain the developmental stage of each colony, some all-day observations have been carried out. In Table 4 are shown each number of foraging trips and of pollen loads brought into nest in each 4 hours of forenoon and afternoon in 6 all-day observations.

OBSERVATION.—On nest A, the more numerous trips were observed in a.m. of Jul. 4 in comparison with Jun. 27. While the ratio of number of pollen loads to the total loads*⁸ collected in a.m. on Jun. 27 was greater than that of p.m. on Jul. 4. A

*⁶ These were clear days with breeze or calm.

*⁷ Here the number of foraging trips in every 30 min. of a day is called "trip density".

*⁸ "Pollen loads" indicate the loads of foragers returned with pollen and nectar or pollen only. "Total loads" include the loads of foragers returned with pollen and nectar, pollen only, nectar only, and nothing.

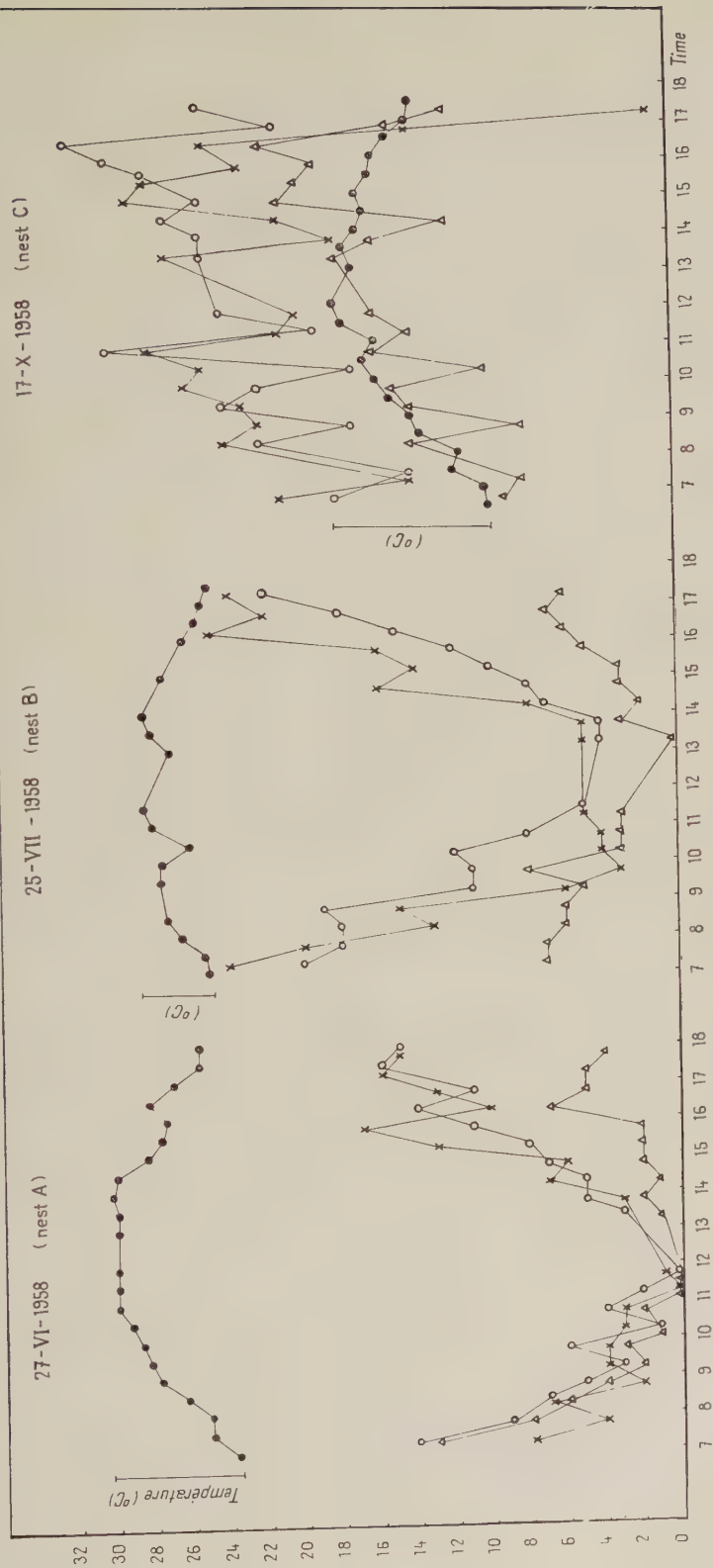


FIG. 1. — Number of foraging trips and temperatures in 30 min. of 3 all-day observations in 3 nests during June to October.

○ - No. departing foragers. × - No. returning foragers. ● - No. pollen loads brought into nest. ● - Temperature (°C).

TABLE IV.—VARIATION OF NUMBER OF FORAGING TRIPS FROM JUNE TO AUGUST.

D—No. departing foragers. R—No. returning foragers. P.L.—No. pollen loads brought into nest*. P.L./T.L.—Ratio of pollen loads to the number of total loads brought into nest*.

	NEST A. 27.VI.1958.				NEST A. 4.VII.1958.				NEST A. 18.VII.1958.			
	D	R	P.L.	P.L./T.L.	D	R	P.L.	P.L./T.L.	D	R	P.L.	P.L./T.L.
Forenoon.	27	37	26	70.3 %	113	130	15	11.5 %	39	61	36	59.0 %
Afternoon.	72	64	22	34.4 %	70	77	48	62.3 %	88	75	7	8.3 %

	NEST B. 25.VII.1958.				NEST B. 22.VIII.1958.				NEST B. 29.VIII.1958.			
	D	R	P.L.	P.L./T.L.	D	R	P.L.	P.L./T.L.	D	R	P.L.	P.L./T.L.
Forenoon.	70	102	41	40.2 %	30	42	29	69.0 %	31	30	17	56.7 %
Afternoon.	113	78	29	37.2 %	39	28	20	71.4 %	56	49	23	46.9 %

remarkable decrease of pollen loads in a.m. of Jul. 4 might be caused by heavy rain. Generally, the pollen collection seems to be disturbed considerably by heavy rain. Further, the decrease of number of trips was recognized in a.m. of Jul. 18.

On nest B were shown the prosperous phase on Jul. 25. But on Aug. 22 (26 days later), the foraging workers decreased remarkably. On Aug. 29, it showed signs of falling of the colony. It is not clear whether these obvious enfeeblements of August nest were caused by unusual high temperature or by parasites as later found when excavated on Sept. 28.

On nest C, a all-day observation was made on Oct. 17. In the forenoon, abnormal behavior of foragers was observed at the nest entrance as shown in late pages. The activities of foragers during 4 hours of this afternoon are as follows: number of departing: 181; number of returning: 213; number of pollen loads brought into nest: 143; and the ratio of pollen loads to the number of total loads: 67.1 per cent. These counts indicate the prosperous or condition near completion phase of the colony. The observation of nest C was continued up to Nov. 8. New females had emerged on Oct. 28. In Table 5, are shown the variations of the number of foraging trips, of the number of pollen loads brought into nest and of the ratio of pollen load to the number of total load during one month from Oct. 9 to Nov. 8. Similarly in the case of other nests, the number of foraging workers increased remarkably in the afternoon of each day notwithstanding a trip duration of each forager was prolonged. This fact seems to be due to extreme increase of foragers in the afternoon. It became subsequently in the observation of marked foragers. The number of foraging trips reduced immediately after the emergence of new females. In early November, the departing of only 2-3 wearily workers were observed in 30 min. In final observation on Nov. 8 were seen only 2 departing and 2 returning by a medium sized and wearily worker in 30 min., Viz., 10:11—return without pollen load, 10:13.5—departure, 10:14.2—return without pollen load, 10:17—departure. Moreover, the trip for nectar of new females decreased gradually in November, and finally only a single new female was observed in 30 min. Since the late October temperature fell down with a run.

D—No. departing foragers. P.L.—No. pollen loads brought into nest*. P.L./T.L.—Ratio of pollen loads to the number of total loads brought into nest*. **—New Females.

	10 : 00-10 : 30					10 : 30-11 : 00					13 : 30-14 : 00					16 : 00-16 : 30				
	D	R	P.L.	P.L. T.L.	D	R	P.L.	P.L. T.L.	D	R	P.L.	P.L. T.L.	D	R	P.L.	P.L. T.L.	D	R	P.L.	P.L./T.L.
9.X.1958																				
10.X.1958	19	14	41*	78.5 %	30	28	23	82.4 %	23	21	21	100.0 %	20	22	22	100.0 %				
11.X.1958	20	22	9	40.9 %	34	26	16	61.5 %					15	15	14	93.3 %				
13.X.1958	27	29	12	41.3 %	30	26	14	53.8 %	27	33	19	57.5 %	17	21	15	71.4 %				
14.X.1958	28	32	17	53.1 %	25	20	10	50.0 %	21	26	19	73.4 %	24	23	20	89.5 %				
15.X.1958				Rain fall					21	31	11	34.7 %								
16.X.1958	29	18	12	66.7 %	24	31	15	48.4 %	20	24	14	53.3 %								
17.X.1958	25	17	7	41.2 %	28	30	14	46.7 %	18	25	15	60.0 %	25	32	18	56.3 %				
20.X.1958	33	26	12	46.2 %	28	30	12	40.0 %					25	23	14	60.9 %				
21.X.1958	25	29	8	27.5 %	29	23	6	26.1 %	24	21	8	38.1 %								
23.X.1958	19	18	3	16.6 %	22	19	5	26.3 %	19	26	8	30.8 %	14	20	5	25.0 %				
24.X.1958					24	27	13	48.1 %					13	21	7	33.3 %				
25.X.1958					24	29	13	44.8 %												
27.X.1958					22	22	10	45.5 %	14	14	11	78.6 %								
28.X.1958					3**	2			0	15	8	53.5 %	4	10	3	30.0 %				
29.X.1958					23	22	12	54.5 %	13	10	7	70.0 %								
30.X.1958					2**	0			1	18	9	50.0 %								
31.X.1958					16	12	5	41.7 %	12	3										
4.XI.1958					1**	0			0**	3	0									
5.XI.1958					5	5	0		2	0	0									
7.XI.1958					1**	0			3	4	0									
									0**	1							1	1	0	
8.XI.1958	2	2	0														0**	0		

5° — Seasonal variation in the body sizes of foragers and in the number of departing foragers with orientation flight.

On 3 colonies, seasonal variations in the body sizes of foragers and also in the number of departing foragers with orientation flights were recorded during from June to November as shown below.

OBSERVATION.—(Nest A) 20.VI.1958 (16 : 15)—The foraging trips of workers with fresh and medium or large-sized bodies were observed. 26.VI.1958 (16 : 00-16 : 30)—Probably newly emerged workers (with fresh and large-sized bodies) departed the nest with orientation flights. Seven marked fresh workers had large-sized bodies except one with small sized. 27.VI.1958 (all-day)—Eleven workers (a.m.-2, p.m.-9) departed with orientation flights. Their bodies were medium or large-sized and fresh. 30.VI.1958 (15 : 50-16 : 50)—Nine workers departed with orientation flights. They were medium-sized workers. 3.VII.1958 (15 : 30-16 : 30)—Five marked workers had fresh and large-sized bodies. 4.VII.1958 (all-day)—Thirty-seven workers (14 in a.m. and 23 in p.m.) departed with orientation flights. Resembling the data from day-long observation of Jun. 27, a large number of the foragers in question were counted in the afternoon. The counts in each 30 min. are as follows, 7 : 30-12 : 00 (a.m.) = (1 ♂) → (0) → (0) → (1) → (0) → (1) → (7) → (2) → (2), and 13 : 30-18 : 00 (p.m.) = (5 ♀♀) → (3) → (2) → (1) → (2) → (2) → (4) → (1) → (3). Out of 37 workers in question, 7 workers had medium-sized bodies and other 30 workers had large-sized bodies. 18.VII.1958 (all-day)—Fourteen workers (2 in a.m. and 12 in p.m.) started with orientation flights. Tendency of increase departing workers with orientation flight was also shown in the afternoon. Depilated workers were also found considerably in this day.

(Nest B) 25.VII.1958 (all-day)—41 workers (19 in a.m. and 22 in p.m.) departed with orientation flights. The larger number of workers in question were observed in the periods of 7 : 00-9 : 00 and after 14 : 00, that is, 7 : 00-11 : 30 (a.m.) = (4 ♀♀) → (4) → (5) → (3) → (1) → (0) → (0) → (1) → (1) and 13 : 00-17 : 30 (p.m.) = (2 ♀♀) → (0) → (3) → (0) → (3) → (2) → (4) → (4) → (4). This 41 workers had almost largesized and fresh bodies.

In general, the most foragers of nests A and B had large-sized and fresh bodies in June and July. But 28 days later, the remarkable changes on body sizes of foragers were recognized in day-long observation on August 22. There were included very small-sized workers such as the first emerged workers in the spring nest or very large sized workers such as new females. Of these workers, the small ones departed as usual with orientation flights. It is supposed that such small sized workers are unaccustomed for foraging trips.

OBSERVATION.—(Nest B) 21.VIII.1958 (all-day)—Fifteen workers departed with orientation flights. 29.VIII.1958 (all-day)—Various sized 20 workers departed with orientation flights. Most workers were a little weary ones. 3.IX.1958 (15 : 00-15 : 30)—The foragers were small sized and weary individuals.

(Nest C) 9.X.1958 (16 : 15-16 : 45)—In the first observation of nest C, the wide-ranged variation in body sizes of foragers were recognized. The most of foragers were large-sized and fresh workers. 17.X.1958 (all-day)—Various sized 50 workers departed with orientation flights.

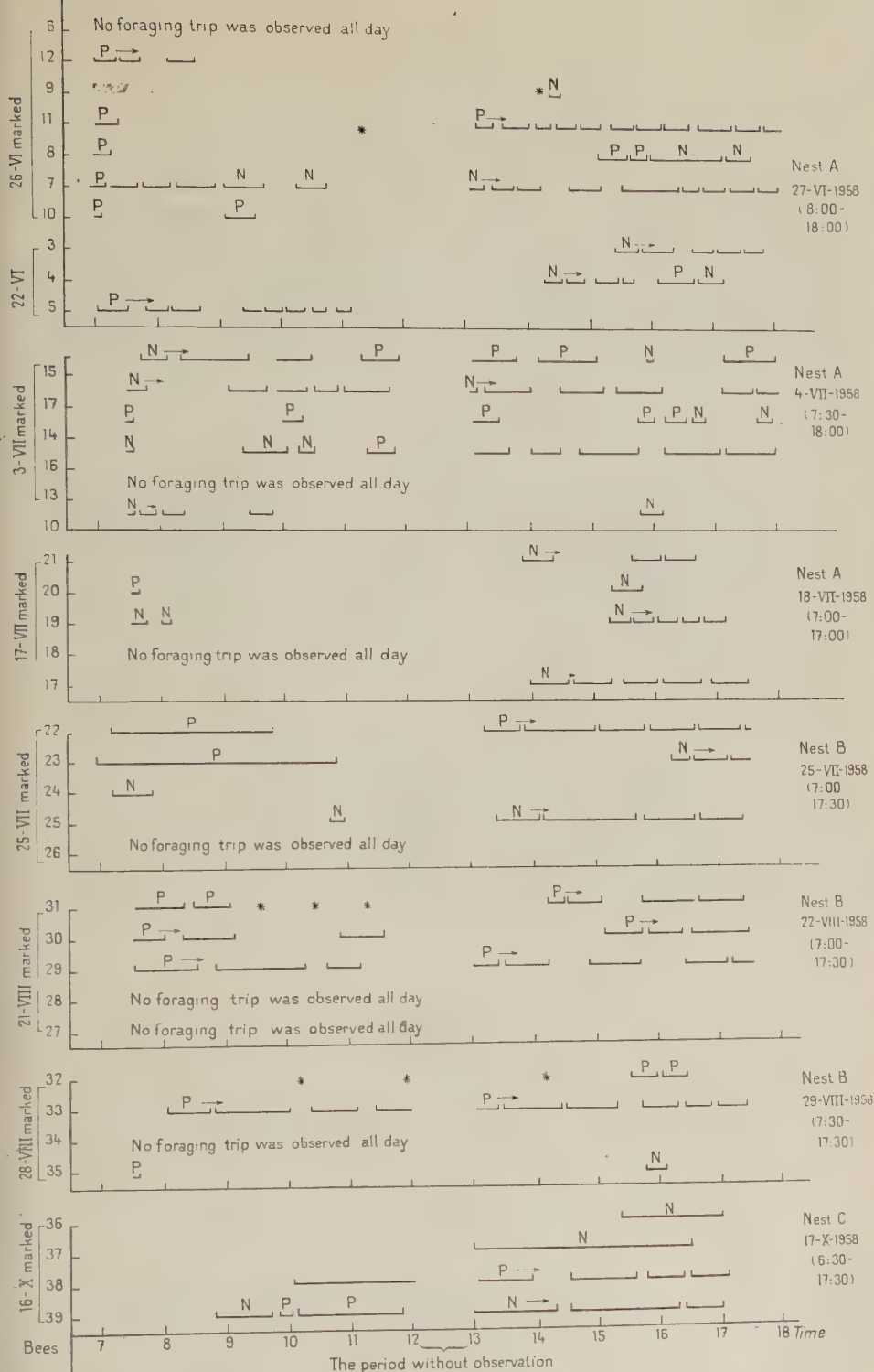


FIG. 2. — Activities of marked foragers of 3 nests in 7 all-day observations during June to October.

* Uncommon behavior or orientation flight not followed by flying away.

Two problems mentioned below seem to be particularly important in these observation results. In nests of June-July, the workers departing with orientation flights were uniformly large-sized and fresh ones. This fact means the addition of newly emerged workers to the original foragers in most cases. On the other hand, in the colonies of last August, September and October, weary workers departed with orientation flights, and they were remarkably small-sized in most cases. Further, the foragers became intermixture of various sized workers since late summer to autumn. Particularly, it has to be emphasized that the very small-sized workers carried out the foraging trips in the colony of the late season (Plate 1). Cumber (1949) also suggested that the smaller workers of a bumblebee colony forage when their colony is dying out.

Another point was observed on the colonies in June-July. The number of workers who departed with orientation flight increased in the afternoon as compared with that in the forenoon. The fact may be related to their behavior as shown below. Newly emerged workers began their foraging trip in the afternoon. Some marked foragers, especially, made their trips always only in the afternoon. Generally, more numerous foraging trips were always counted in the afternoon than in the forenoon.

6° — *Foraging of marked bees.*

All-day observations—The activities of marked workers were observed in detail. In Fig. 2 are shown the activities of marked foragers of 3 colonies in 7 all-day observations on June 27, July 4, 18, 25, August 22, 29 and October 17. The individualities in them were distinctly recognized on the following points, i.e., grade of constancy in foraging duty, difference in starting or finishing time of trips and difference in total number of trips in day-long.

Some workers were not found to forage throughout a day notwithstanding they had been engaged in forage at the time of marking. At nests A and B some workers flew out of nest only to make orientation flight and not to fly away for forage.

Inconstant foragers worked sometimes only in every afternoon. Also in the colony of *ardens*, a similar phenomenon had been observed as already reported (Miyamoto, 1957 a, b).

Continuous observation on marked workers was difficult, especially in August. Longevity of foragers seems to be shortened under high temperature in summer.

The grade of constancy in foraging of each marked worker are shown in Fig. 2. For example, the workers of nest A Nos. 1 and 5 worked as pollen collector more than 80 per cent and 70 per cent of the bee-days respectively, while No. 39 of nest C worked as pollen collector in all the bee-days.

Duration of foraging trips—The durations of trips for pollen and

nectar collections*⁹ required about 15-30 min. and 15-25 min., respectively, similarly in the case of *ardens* (Miyamoto, 1957 *a*). While, the times needed to deposit the pollen or nectar inside of nest were 2-6 min. or



PLATE 1. — Foragers (1, 2) and new female (3) of autumn nest C of *Bombus diversus*.
1, Small-sized foragers; 2, Large-sized foragers; 3, New female.

2-4 min. in most cases, respectively. In this species, the needed time for deposition of the loads was longer than in *ardens**¹⁰.

The durations of trips for pollen and nectar became longer gradually with the lapse of time from July to October. Particularly an irregular prolongation was observed on October 17.

7° — Direction of flight in departure.

Data from all-day observations—The direction of flight when foragers left their nest was noted in nests A and B. Both nests were situated in

*⁹ Foragers returned with pollen loads are shown as pollen collectors, and without pollen loads are presumed to be nectar collectors.

*¹⁰ It is supposed that this fact was caused by the difference of nest structures of both the bumblebees.

about central part of open rice fields. The distribution of the direction in question, and its change with the lapse of time on 6 all-day observations are as follows.

OBSERVATION.—At nest A, number of workers in respective direction in day-long of Jun. 27 were as follows: 42 ♀♀ (north) > 33 (south) > 19 (west) > 12 (east) > 11 (southwest) > 8 (southeast) > 1 (northeast). North and south were the directions adopted by most of workers. The data of Jul. 4 indicated a different tendency, that is, 82 ♀♀ (s-w) > 62 (w) > 32 (s) > 28 (n) > 7 (e-n) > 5 (e) > 3 (s-e). The observations on Jul. 18 differed, that is, 45 ♀♀ (n) > 22 (e) > 21 (s) > 20 (s-w) > 6 (e-n) > 3 (s-e) > 2 (s-e).

At nest B, situated at a point of 10 m. apart from the nest A, the observation results are as follows. On Jul. 25, number of departing workers and direction were 85 ♀♀ (n) > 68 (s) > 16 (w) > 9 (n-e) > 8 (s-e) > 7 (e) > 2 (s-e). Both north and south were more dominant. After 15:00 of this day departing toward north increased markedly. This fact may mean the plenty of pollen and nectar sources in area of respective direction at respective time. On Aug. 22, also a result similar to that of Jul. 25 was obtained at the nest B, that is, 27 ♀♀ (n-e) > 23 (s) > 5 (w-e). On Aug. 29, further, there was also found the similar tendency to that of Aug. 22.

Constancy of direction when marked workers left their nest—On June 23, each marked worker had its particular direction in departing nest. Moreover, they indicated the constancy in each direction for consecutive days.

OBSERVATION.—A pollen collector No. 5 showed a remarkable constancy to the western direction all-day on Jun. 27. Moreover, she kept this direction probably during several successive days, it was confirmed at least in 6 days. Other instances are as follows. Worker No. 16 departed constantly to the southern direction all-day on Jul. 4; Worker No. 19 showed intensive constancy to the northern direction in all-day's trips on Jul. 18; No. 25 in the southern direction and Nos. 22 and 23 in northern course all-day on Jul. 25; On Aug. 29, worker No. 33 departed constantly in the northeastern direction.

Foraging area—The worker foraged sometimes near her nest. For example, at 17:34 of June 23 (nest A), a worker No. 5 successively visited the thicket of *Prunella vulgaris* L. at roadside of 2-3 m. apart from nest. Up to 17:37, she visited the *Prunella* flowers for collecting nectar, and 17:37.5, she was found on the flowers of *Cirsium japonicum* D.C. near *Prunella* thicket. But after this, she removed once more to *Prunella* and continued the nectar collection. As another instance, a worker flew away in straight up to a point of 4-5 m. apart from nest at 16:00-17:00 of June 30, and visited successively the flowers of *Cirsium japonicum* D.C. for 7 min.

In several occasions, pollen collectors are observed to suck nectar by their way home near their nest entrances. A worker (nest B) with good pollen load in her way home arrived at nest after suck nectar for 2 min. from the flower of *Lespedeza bicolor* Turcz. var. *japonica* Nakai at a point of 1.5 m. apart from nest.

8° — *Miscellaneous behaviors of workers.*

Unusual behavior of workers in departure—As shown in Fig. 2, some workers of nests A and B flew out from the nest entrance and made the orientation flight but did not fly away and entered into the nest at once.

OBSERVATION.—For instance, at nest A, in all-day observation of Jun. 27, worker No. 11 remained in the nest for 4 hours after the last foraging trip for pollen. At 11 : 14, she flew out from nest entrance, and made the orientation flight, but she did not fly away and entered into the nest entrance at once. Further, after 220 min., at 13 : 05, she departed normally (without orientation flight) and made 11 pollen collecting trips till 17 : 43.

Another example was observed at nest B. On Aug. 22 (all-day observation), worker No. 31 carried out 6 pollen collecting trips (2 in a.m., 4 in p.m.). But she made above-mentioned unusual behavior on the nest entrance 3 times at 9 : 37.5, 10 : 25.5 and 11 : 16.2. In worker No. 32 at nest B, was also observed the same behavior 3 times at 10 : 30, 11 : 57 and 14 : 07.5 on Aug. 29 (all-day observation) and after 15 : 30, she carried out 2 trips for pollen.

In autumn nest C, more curious behavior of workers was observed frequently. Some fresh workers crawled out from the nest entrance and tried to fly up 2 or 3 times, but they all failed. After this, they entered into the nest once more. It seems partly that this behavior have some correlation with the lower temperature in middle October. Such behavior of workers in autumn nest C somewhat differed from the like behavior mentioned above in the nests A and B.

Abandonment of larva from nest—Abandonment of larva from nest by workers was sometimes observed in the nests of *ardens* under unfavorable nest conditions (Miyamoto, 1957 *a*) or in the final period of nest (Miyamoto, 1957 *b*) as reported previously. This phenomenon was also observed in the present species at nest C in October.

OBSERVATION.—At 10 : 22, 13 : 44.8 and 16 : 03 on Oct. 10, 3 medium-or large-sized workers departed with larvae in their mandibles from the nest. Next day, on Oct. 11, at 10 : 28, a medium-sized worker departed also with a larva. At 10 : 04 of Oct. 14, a large-sized worker departed with a larva. This worker was caught by net at once and was dissected. There was found no tendency to develop in ovary as in the case of *ardens*. Another fresh and medium-sized worker departed with large-sized larva at 10 : 14.5.

It seems that this phenomenon may have similar meaning to carrying away the larvae from nest by some social wasps such as *Vespa* late autumn.

Repetition of return—Some unusual behavior of the workers was observed from 7 : 30 to 8 : 30 on October 17 (all-day observation in nest C). Some workers returning with pollen failed to reach comb. Probably some obstacles existed in gallery leading to the comb. They remained near the entrance for a while and then went back a way to their field, after 2 or 3 times of orientation flights. Again they returned and, being repelled, flew away once more. This returning was repeated many times as observed and recorded by many authors in solitary wasps and bees when interrupted to enter into nest.

Unusual departing of workers from nest—After observations just mentioned, from 7:37, workers of different sizes appeared at entrance crowding against and departed with orientation flights. For 10 min. of 7:37-7:47 came out 14 workers, out of which only 7 made orientation flights. After this, the activity of foragers became normal, but at 8:08.5, a worker departed with a larva in her mandibles. The reason for this remains unknown.

Clinging of *Antherophagus nigricornis* Fabricius to the worker—At 8:30.2 of October 17, a large-sized worker departed with *A. nigricornis* Fab. which attached to her neck. Both insects were caught at once by net. *Nigricornis* intensely clung to the worker's body even in glass tube.

Carrying-out pebbles from nest—At 9:32 of October 17, a large-sized and weary worker departed with a pebble in her mandibles. The worker was caught by net. The fact was also observed in final period of an *ardens* colony (Miyamoto, 1957 *b*).

Summary.

1. In general, the female after hibernation appears late in April, the workers in middle of May, and new females and males in September-October. Their nesting life ends early or middle November in Sasayama, Hyogo. Pref., Japan.

2. The females just appeared from their winter-quarters had quite undeveloped ovaries. Their pollenomeliphagous habit seems to bring up their ovaries to mature condition. And after maturation of ovaries, they started to search for nesting site.

3. The flowers visited by founding females appeared in spring and by workers are shown in Tables 1 and 2, respectively.

4. The curve plotted by the number of foraging trips in each 30 min. by all-day observations up to August was V-shaped. The curve is similar to the typical curve of that in *B. ardens* and indicates a converse correlation between trip density of workers and atmospheric temperatures. On the contrary in autumn colony, the number of foraging trips increased paralleling with rising temperatures. No other seasonal variation were recognized on the foraging activity during June to October.

5. All of the foraging workers observed during June-July were almost medium or large-sized and fresh individuals. But in late August, the variation range of body size of forager became wide, and the large-sized workers were accustomed to foraging trips, while the small-sized workers departed with orientation flights in most cases.

6. Concerning the personnel of workers departed for foraging trips with orientation flights, some differences were found between the prosperous colony of June-July and the final colony just before collapse in October. The former workers were medium or large-sized and fresh ones, but, on

the other hand, workers of the latter colony in *finale* were small-sized and wearily individuals in most cases.

7. The durations of trips for pollen and nectar were 15-30 min. and 15-25 min. respectively. On the other hand, the times required to deposit pollen and nectar loads were 2-6 min. and 2-4 min., respectively.

8. Direction of flight in departing workers was fixed in each individual. Constancy of this direction of each forager in day-long or successive days'-observation was remarkably.

9. Abandonment of larvae by workers from nest was recognized in the autumn nest just before emergence of new females.

Résumé.

— Après l'hibernation, les femelles apparaissent à la fin d'avril, les ouvrières au milieu de mai et la nouvelle génération sexuée en septembre-octobre. La vie du nid se termine au début ou au milieu de novembre à Sasayama.

— Les femelles sortant de la période d'hibernation ont des ovaires très peu développés. Leur régime floricole amène leurs ovaires à maturité. Ensuite elles cherchent un lieu de nidification.

— Les fleurs visitées par les fondatrices et les ouvrières sont mentionnées dans le texte. La courbe traduisant le nombre de sorties de récolte par périodes de 30 mn dans des observations quotidiennes poursuivies jusqu'au mois d'août est une courbe en V. Cette courbe est semblable à la courbe typique de *B. ardens* et elle montre une corrélation inverse entre la densité des voyages des ouvrières et les températures. Au contraire, dans la colonie automnale, le nombre de sorties croît en même temps que les températures. Aucune autre variation saisonnière n'a pu être remarquée concernant l'activité de récolte dans la période de juin à octobre.

— Toutes les ouvrières récolteuses observées pendant juin et juillet sont des individus frais de taille moyenne ou grande. Mais, à la fin d'août, les différences de taille entre les récolteuses croissent et les plus grandes ouvrières sont plus spécialement observées dans les récoltes à grandes distances, alors que les plus petites se remarquent au point de départ des vols nuptiaux.

— La durée des voyages de récolte de pollen et de nectar sont respectivement de 15-30 mn et de 15-25 mn. Les temps de dépôt du pollen et du nectar sont de 2-6 et 2-4 mn respectivement.

— La direction du parcours des ouvrières est fixée individuellement. La constance de la direction de chaque ouvrière pendant un ou plusieurs jours est remarquable.

— Au moment de l'éclosion des nouvelles femelles à l'automne, les larves du nid sont abandonnées par les ouvrières.

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**BIOLOGY OF THE PRIMITIVE SOCIAL BEE,
HALICTUS DUPLEX DALLA TORRE II.
NEST STRUCTURE AND IMMATURE STAGES (I)**

by **Shōichi F. SAKAGAMI** and **Kazuo HAYASHIDA**
(Zoological Institute, Hokkaido University.)

The nest structure of this species has been briefly touched upon in the previous paper which described the general outline of the life history (Sakagami & Hayashida, 1958). The species exhibits, however, a highly developed architectural technique as in the famous earthen comb maker, *Halictus quadricinctus* Fabricius (Verhoeff, 1897) and certain Neotropical species (Claude-Joseph, 1926, Michener & Lange, 1958, *a, b, c*). Therefore, the description of the nest structure will be given in the present paper in detail, from both static and dynamic viewpoints, together with illustrations of various nest patterns. As adequately pointed out by Baerends (1941), countless publications on the biology of various Aculeata are based upon few or fragmentary observations. The generalizations derived from such studies may occasionally lead to dangerous false interpretations. In biologically important groups such as *Halictus*, it seems legitimate to describe fully the mode of life, based upon a large number of observations, at least in some representative species. In connection with the arrangement of immature stages within nests, morphological descriptions will be added along lines recently established by Michener (1953, 1954).

Descriptions are mainly based upon the nests taken from an aggregation inhabiting the University Botanical Garden in Sapporo, especially upon 187 nests excavated in 1957, for these were examined in full detail. Some additional, often important information was also obtained from 38 summer nests excavated in 1954, and from 104 spring and 73 summer ones in 1958.

Dates of excavation of these nests are as follows :

1956 (All summer nests) : Nos. 1-3 (July 31), 4 (August 1), 5-7 (Aug. 10), 8-11 (Aug. 15), 12-16 (Aug. 16), 17-19 (Aug. 22), 20-23 (Aug. 30), 24-26 (September 6), 27-28 (Sept. 19), 29-38 (October 13).
1957 (Spring) : Nos. 39-47 (April 25), 48-54 (May 2), 55-64 (May 8), 65-74 (May 16), 75-84 (May 23), 85-94 (May 30), 95-106 (June 5), 107-115 (June 12), 116-125 (June 19), 126-135 (June 26), 136-139 (July 3), 140 (July 10).

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1957 (Summer) : Nos. 141-152 (July 10), 153-164 (July 13), 165-173 (July 18), 174-181 (July 24), 182-189 (July 31), 190-205 (August 7), 206-209 (Aug. 14), 210-213 (Aug. 16), 214-221 (Aug. 21), 222-225 (September 4), 226-227 (Sept. 18).

1958 (Spring) : Nos. 228-236 (April 24), 237-244 (May 9), 245-258 (June 20-21), 259-310 (June 24-26), 311-330 (July 1 and 2).

1958 (Summer) : 331-338 (July 12), 339-353 (July 15-16), 354-363 (July 21), 364-370 and 379-381 (July 24), 371-378 and 382-390 (July 28), 391-401 (July 30), 402-405 (September 2).

Among these nests, the following ones are the old remains of the preceding year's summer nests : Nos. 44, 54, 57, 73, 77, 116, 135, 222 and 246. Except for a few nests opened in 1956 at the start of present study, the excavation was all done without using plaster of Paris, paraffin, etc., because the soil texture was so amical that burrows and cells could be, in most cases, relatively easily traced.

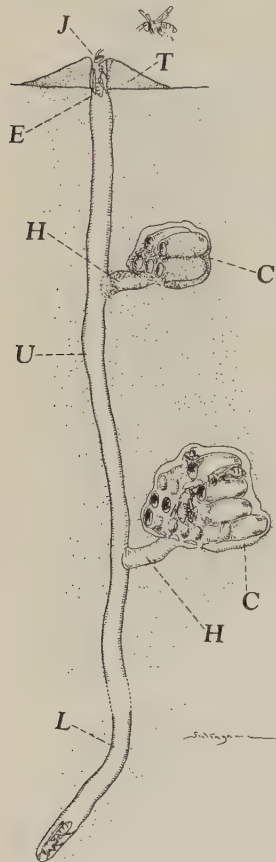


FIG. 1. — Summer nest with old spring cavity filled with soil. *J* : Junitor. Other abbreviations see in text.

I. — NEST STRUCTURE

As mentioned previously (Sakagami & Hayashida, 1958), this species has each year two active periods, one in spring (late April to May) and the other in summer (July to early August). But the nest burrow used in both periods is, as a rule, one and the same and consists of the following elements:

T : Tumulus at the entrance.

E : Entrance and adjoining constricted part at the top of nest burrow.

U : Upper shaft. Here conveniently defined as the upper part of the main burrow between the entrance constriction and the point of connection of the horizontal lateral. Or, in the younger nests in which the horizontal lateral is still absent, the whole main burrow below the entrance is called upper shaft.

H : Horizontal lateral gallery connecting *U* and cell cluster.

C : The first (*C*₁) and second (*C*₂) cell clusters. The latter is absent in spring nests, often but sometimes present in summer ones.

Ca : Cavities surrounding *C*. Absent at the initial stage of *C* construction.

L : Lower shaft. Here conveniently defined as the part of the main burrow below the junction with *H*. In the younger nests before issuing *H*, *L* is absent by definition.

Arrangement of the various elements in a general plan as shown in Fig. 1 varies but little between two active periods. The terminology proposed by Malyshev (1936) in his treatise on bee biology will be adopted in describing the types of nest elements (shown by italicized word in the discussions below).

1. 1. *Tumulus (T) and Entrance (E).*

The formation of tumulus, an accumulation of soil deposits surrounding the nest entrance, is caused by a specific trait common to most halictids, namely, the absence of a tendency to remove the excavated soil particles from the surroundings of entrance. As the active digging is usually

TABLE 1. — SEASONAL CHANGES IN DIMENSIONS OF TUMULI IN 1957.

DATE.	NUMBER OF NESTS.				DIMENSIONS OF TUMULI (mm) (*).			
	Open		Closed.	Total.	Diameter.		Height.	
	with <i>T</i> .	without <i>T</i> .			Mean.	Range.	Mean	Range.
IV 25	9			9	38	30-50	16	0-30
V 2	6	1		7	29	25-45	7	7-10
8	7	3		10	29	0-45	4	0-7
16	3	1	3	7	30	25-35	16	10-20
23	2	5	1	8	13	0-25	6	0-13
30	1	1	7	9	46	46		
VI 5			12	12				
12			9	9				
19			10	10				
26			10	10				
VII 3			5	5				
10	6	3	3	12	28	15-35	3	0-15
13	6	1	5	12	42	25-70	10	8-25
18	8	1	1	10	38	23-55	9	0-15
24	6	1	1	8	43	35-50	4	0-10
31	6	1		7	24	6-40	10	—
VIII 7	2	1	13	16	24	0-45	0	
14			4	4				
16		1	3	4				
21	4	4		8	25	0-55	5	0-12
IX 4			4	4				
18			2	2				

(*) Nests without *T* were not considered.

performed during the night, nests in initial stages often show a large *T* in morning. Such fresh *TT* are characterized by the massive surface contour consisting of wet, rough soil particles (Fig. 2 *a*) but they gradually become conical elevations as a result of drying and flight activities (Fig. 2 *b*) before the final disappearance (Fig. 2 *c*). Table 1 shows the seasonal changes in dimensions of *TT* and the number of nests with and without tumuli, corresponding to the two activity periods (Cf. Fig. 1 in Sakagami and

Hayashida, 1958). When *T* is still fresh, its inner walls are often smoothed by means of the abdominal tip.

Although the tumulus occasionally tends to become slightly *eccentric* and *asymmetrical*, it is principally *radial* and *central*, that is, with the entrance hole just in its center and symmetrical about any vertical plane passing through the center. This accords with the absence of any preferred direction in throwing out the soil particles or in departure and return flights. This species makes no special entry architecture as in some allied species. If the entrances of two nests close to each other, they often later possess a common conical *T* due to the flight activities of inhabitants of both nests (Fig. 2 *a* to *c*). The tumulus is open during the daytime and closed in night, but, under adverse weather conditions, either rainy, or windy, or too hot, it is partially open or closed even in daytime.

Constriction of the nest entrance seems to be a trait common to halictids and is associated with the occurrence of guardianship, another group-specific trait. The constricted part in *H. duplex* extends 0.8 to 1.8 cm from the entrance, but an abnormal case was seen in Nest 380 (Fig. 33), in which the diameter of *U* remained 3 mm until 45 mm below the surface and became 5 mm thereafter. If the entrance possesses a well developed *T*, the constriction is either limited within *T* alone, or continues downwards into the firm earth layer. If the constriction is artificially destroyed, it is repaired within a short time. On April 30, 1959, the entrances of 20 nests were enlarged with a pencil to about 6 mm in diameter. By the next morning, the entrances were constricted to 3-4 mm in diameter except

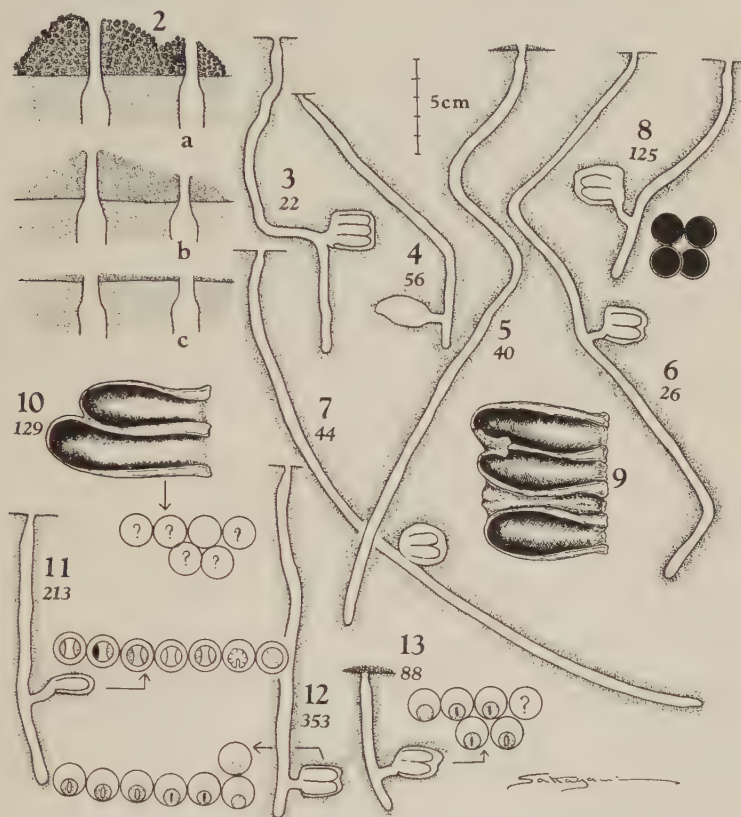
TABLE 2. — DIAMETER OF ENTRANCE AND MAIN BURROW (mm).

DIAMETER	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	8.0	Total.
ENTRANCE												
Spring	1	1	3	16	14	2	3					40
Summer		7	25	16								48
MAXIMUM												
Burrow						4	25	6	10	2	3	50
Diameter												

for 3 nests, which were apparently abandoned. As seen in Table 2, the diameter of entrances showed a slight but significant differences between spring and summer nests. It is probable that the difference is related to that of body size of guard bees. The spring nests are not naturally guarded by bees other than the large mothers. But the guards of summer nests are mostly lesser daughter bees, although the participation of still surviving mothers in the guard duties was occasionally observed.

1. 2. *Upper shaft (U) and horizontal lateral (H).*

Below the entrance constriction, the diameter of burrow varies but little throughout *U* and *L* and between spring and summer nests (Table 2). No correlation was found between diameter of *E* and that of *U* or *L*.



FIGS. 2-13. — Change of tumulus, form of cell and some examples of the course of main gallery and cell arrangement. Throughout these and subsequent figures, italic letters given to each figure show the nest number and the scales indicate the relative depth of cavities and shaft alone, not always the diameter of shafts, cells and cavities. Developmental stages in each cell are schematically represented (Compare with Section 2. 3. in text and Fig. 79).

Occasionally, the burrow has a larger diameter (up to 8 mm), usually near the point where *U* and *H* join.

Although both *U* and *L* are irregularly bent or elbowed, the general trend through these windings is distinctly vertical and downward. Any attempts to find regularity in the direction and frequency of winding seems to be futile and unnecessary. Some examples may be seen among the accompanied figures, with remarkable cases in Figs. 3-7 and 59. As seen

from these figures, the initial part of gallery descends nearly vertically in most cases. There is no differentiation of main burrow into the rather horizontal *entrance canal* and the vertical *descending section* as in many digger-bees other than *Halictus*.

The inner walls of the main burrow are often smoothed by the mere

TABLE 3. — FREQUENCY DISTRIBUTION OF DEPTH OF JOINT *U* — *H* AND OF BOTTOM OF CAVITY

	DEPTH (cm).	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	30
JOINT.	Spring (*)	4	1	3	9	13	13	14	6	4	5	1	2	1													1
	Summer (1956, 1957)			1	1	2	3	5	3	11	13	8	9	9	11	4	7	3	1	1	1	1	1		1		
	Summer (1958)								1	1	1	1	3	4	5	6	2	1	4	2	2	3	2		1		
BOTTOM OF CAVITY.	Spring (1957)			2		12	9	7	4	6	3	3	1	3	2	1											
	Spring (1958)				2	5	8	10	7	3	1			1													
	Summer (1956, 1957)			1		1	4	5	5	9	6	9	5	8	4	6	5	7		3		1	2		1		1
	Summer (1958)							1	1	1	4	1	5	9	6	1	4	3	6	9	2	4	2	2	1	1	1

(*) Depth of Joint in Spring nests was not measured in 1958.

movements of the inhabitants. No special coating in any sense exists on the walls of *U*, *L* or *H*.

The depth at which *H* arises differs markedly between spring and summer nests. This corresponds to the difference in depth of spring and summer *CC* (Table 3). The summer nests in 1958 showed a definite tendency for *H* to be deeper than in previous years, probably because of the dry and hot weather in that year. The diameter of *H* was approximately equal to that of *U* in 34 nests examined on this point. *H* runs mostly horizontally, often ascends, but rarely descends from *L* to *Ca* (Table 4). It is still not clear whether this rarity of descending inclination has any adaptive significance or not.

The length of *H* is 8-14 mm in spring nests, and 4-10 mm in summer ones, without significant differences between two periods (Table 4). Although not included in the table, abnormally long *HH* were observed in two experimentally transplanted nests, Nos. 391 (35 mm) and 396 (40 mm). Course of *H* is usually straight, but in occasions bends irregularly as in Nests 78 (Fig. 75), 125 (Fig. 8), 140 (Fig. 39), 147 (Fig. 108), 189 (Fig. 119), 191 (Fig. 125) and 391. No correlation exists among length, inclination and course of *H*.

In young nests with only a few cells, *H* opens directly to these cells. But in more advanced nests, *H* opens to *Ca*, mostly to its lower half, irrespective of cluster size (Table 5).

TABLE 4. — INCLINATION AND LENGTH OF HORIZONTAL LATERAL BURROW (*H*).

TYPE OF INCLINATION.		A	B	C	D	E	Abnormal.		Total.						
Spring.		10	6	30	3	1	3		53						
Summer.		11	7	46	6	2	3		75						

LENGTH (mm).	<2	2	4	6	8	10	12	14	16	18	20	22	24	26	Total.
Spring.	7	0	4	6	10	17	1	9	4	3					61
Summer.	11	3	11	11	10	17	7	2	6	1	3		3	1	86

TYPE OF INCLINATION. — A : Distinctly ascending from *L* to *Ca*. — B : Slightly ascending. — C : Approximately horizontal. — D : Slightly descending. — E : Distinctly descending.

This fact corresponds to the order of cell construction, which starts from the cavity bottom and proceeds upwards as mentioned later in 2.3.

TABLE 5. — RELATIONSHIP BETWEEN SIZE OF CELL CLUSTER AND POSITION OF JUNCTION *H* — *Ca*.

CLUSTER SIZE MEASURED BY NUMBER OF HORIZONTAL CELL LAYERS (Cf. I. 3, 2.)	<i>H</i> OPENS <i>Ca</i> APPROXIMATELY AT THE LATTER'S WEG						TOTAL
	Upper part.		Middle part.		Lower part.		
	Spring.	Summer.	Spring.	Summer.	Spring.	Summer.	
2		4	10	6	14	17	51
3		1	7	6	10	19	43
4						5	5
5					1		1
6				1		4	5
7		1				2	3
8						1	1
Total.	0	6	17	13	25	48	107

1. 3. Brood cells.

1. 3. 1. Form, size and number of cells.—The form and size of the brood cells are fairly constant, without seasonal differences such as were reported by Legewie (1925) in *Halictus malachurus* Kirby. The cells are *elongate*, i. e., with the longitudinal axes distinctly longer than horizontal and vertical ones, *oval*, *homomorphous*, *bilaterally symmetrical* in the sagittal plane, the bottom usually flatter than other surfaces. The inner wall is *autotichal*, or especially elaborated by saliva, without utilizing any exogenous building material (*endostoechal*), smooth and highly polished except for the neck region. The lining is, however, so thin that it cannot be completely separated. After dessication, the cell cluster becomes very hard. After oviposition, the cells are closed by means of *permeable* soil mass which is so *loose* that it often falls away if the cells are violently shaken with their openings down. The cell closure does not always take place immediately after oviposition, in contrast to most other solitary bees (*Cf.* 2. 4.)

The length of cells is about 12-13 mm and the inside width 6-6.5 mm at the widest part, 3-4 mm at the neck. The cell wall is thinnest at the posterior end, often only 1 mm. Abnormal cells were discovered in two occasions: An elongate cell in Nest 129 (Fig. 10) and a short, round one in Nest 101. The former case is interesting, because its apex protrudes from the posterior surface of *C* (formed by the apices of other cells), but the opening lies just on the anterior surface. This suggests a probable architectural adjustment of the initially mis-directed plan, although the lack of such adjustment is rather frequent as described in 1. 3. 2.

In the preliminary report, the cell number per nest were reported as 1-9 (usually 3-5) in spring, usually 4-7, but often more than 20 in summer. At that time, the number was given based upon the counts of all nests examined. It is obvious, however, that this does not always mean the true cell number of *normal* nests constructed by this species, because many of nests examined were either in the stage of cell building or were abandoned before being completed for various causes. In Table 6, therefore, the cell number was given with respect to the nests which seemed to be normally completed, excluding nests with still imperfect cavities, with eggs and pollen balls, and those with definite marks of abandonment such as the dead owners or heavy infestations by mould or parasites. Even after this correction, some nests with only two to three cells are perhaps still incomplete.

As seen in the table, spring nests contain usually 4 to 6 cells. On the other hand, the cell number of summer nests shows, although distinctly more numerous than in spring, a markedly wide range from 3 to 41, with a very irregular frequency distribution. This large fluctuation, apparently caused by the complex gregarious life, suggests the relatively instable condition of summer gregarism in this species. Further investigations of this problem in related species may be very interesting in connection with

TABLE 6. — NUMBER OF CELLS PER NEST (Some experimentally treated nests excluded).

No. CELLS.	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	18	20	21	22	23	25	30	36	41
Spring 1957	2	5	13	8	9	5	5																	
1958	6	6	16	16	8	6	5	1	1	1														
Total.	8	11	29	24	17	11	10	1	1	1														
Summer 1956, 1957																								
1958		1	3	3	6	6	4	6	5		2	3	1	2	3		1	3		1		1		1
				1		3	1	1	1	2		2	1			3		1	4		1		1	
Total.		1	3	4	6	9	5	7	6	2	2	5	2	2	3	3	1	4	4	1	1	1		1

the stability of social life. At any rate, the wide fluctuation results in difficulties in censusing the population trend of this species. It must be mentioned that the table shows the total number of cells in each nest. The intra-nest cell distribution in nests with two summer cavities will be discussed in Section 2. 6.

1. 3. 2. Arrangement of cells in C.—One of the most characteristic features in the nest structure of *Halictus duplex* is the earthen cell cluster or comb (Figs. 1, 129-131). All cells in the same *C* are built closely in contact with each other. The distance between the inner walls of two neighbouring cells is usually less than 2 mm, occasionally only 1 mm. The longitudinal axis of each cell is, as a rule, slightly *inclined downwards* to the cell opening; Vertical planes through the axes of the cells are parallel; horizontal planes are slightly divergent from each other toward the posterior ends of the cells. Consequently, the front of *C* (formed by the openings of the cells) is weakly concave, and the back convex, but in a degree far less conspicuous than in nests of *H. quadricinctus* Fabricius (Verhoeff, 1897) or *H. chilensis* Spinola and *H. glabriventris* Friese (Claude-Joseph, 1926; on the scientific names of these Neotropical species, see in Sakagami & Michener, in preparation).

Although the vertical arrangement of the cells is often very irregular, each *C* can be arbitrarily divided into several horizontal cell layers. The relationships between the total number of cells in a *C* and the number of cell layers, and that between number of cell layers and the position (counted from the bottom layer) of the largest horizontal cell layer (the layer with maximum cell number) are shown in Table 7 and 8 respectively (In two-cavity nests, each *C* is regarded as an independent case).

Two facts are obvious from these data: 1. Both the number of cell layers and the cell number in the largest layer of course increase with the increase

TABLE 7.—RELATIONSHIP BETWEEN TOTAL CELL NUMBER IN EACH NEST AND NUMBER OF CELL LAYERS.

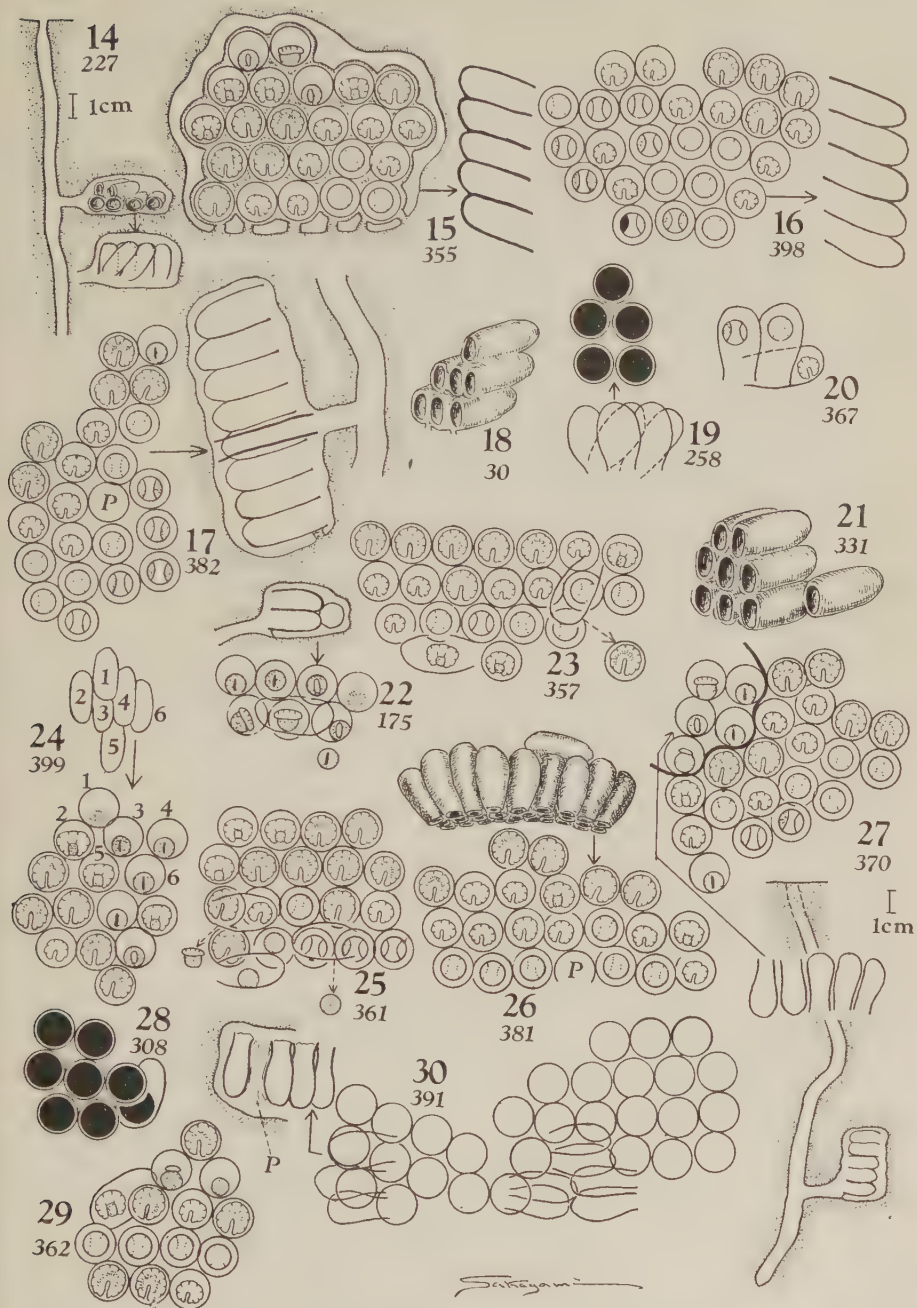
No. Cells.		2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	20	21	22	23	24	25	26	31	35
NUMBER OF CELL LAYERS.	1	2																									
	2	8	7	17	5	1		2		3																	
	3		16	3	18	9	5	5	7	3	1		1	1													
	4			3		5	4	4	3	3		3	3	1	1	1		1		1	3						
	5						1			3	3			1	1	1	1	3	1			1		1	1		
	6															1		1				1					1
	7						1								1					1	1		1		1	1	
	8																										

of total cell number, but only up to 5-6 layers (or cells). 2) The maximal cell number is found usually in the second or third layer from the bottom, hardly ever in the bottom or top layers. Both facts suggest the occurrence

TABLE 8.—POSITION OF THE LARGEST CELL LAYER AND ITS CELL NUMBER.

		ORDER OF THE LARGEST CELL LAYER (*).						
		1st	2nd	3rd	4th	5th	6th	7th
NUMBER OF CELLS IN THE LARGEST LAYER.	2	37	40					
	3	20	29	18				
	4	11	15	10	5			
	5	1	6	5	2	1		
	6		2	4	1	3		
	7		2	3			2	
	8		1	1	1	1	1	
	9		2	2	1	1	1	

(*) Numbered from the bottom layer upward. If the maximal cell number per layer is represented in more than one layer, each was independently counted as one case.



FIGS. 14-30. — Variability in cell arrangement (P: Intercellular passway).

of rudimentary spatial economy corresponding to the rule of minimal surface-mass ratio. Examples of various arrangements are illustrated in the figures together with the disposition of immature stages within cluster (Cf. Fig. 79 and Section 2.3.). Some depatures from spatial economy are seen in Figs. 11 and 12.

The above description gives, however, only the general architectural plan characteristic of species. Departures from this normal pattern are frequently observed as follows:

a) *Mal-orientation of the whole C.*—Three abnormal cases were found. In nests 227 and 380, the clusters were at least partly directed at right angles to *H* (Figs. 14, 33). In Nest 57 (Fig. 44), the whole *C* was situated diametrically opposing to *H*. In this case, it is hard to imagine how the *C* was constructed.

b) *Angle between longitudinal cell axis and horizontal plane.*—As mentioned above, the longitudinal cell axis, as a rule, is *slightly inclined* downward from the posterior to the anterior surface of the cluster (in an exaggerated manner in Nest 355, Fig. 15), although the horizontal orientation, of axes is not rare. On the other hand, the reversed inclination, *inclined upwards*, was observed in its typical expression only in two instances (Figs. 16 & 17).

c) *Relationships among horizontal cell layers.*—Fundamentally, front and back of *CC* are approximately vertical, for the openings of the cells lie in a common vertical plane. But the slight inclination caused by the backward construction of upper cell layers is very frequent and occasionally gives a fairly distorted appearance to *C* as in Fig. 18. It may be soon recognized that this inclined pattern of the cell cluster corresponds to the normal cell orientation, *inclined downwards*. Contrarily, the reversed inclination, the forwarded construction of upper layers, was never observed. Crossing of longitudinal axes between two horizontal layers was observed in Nests 227 (Fig. 14), 258 (Fig. 19) and 367 (Fig. 20).

d) *Irregular orientation of individual cells within C.*—The forwarded or backwarded positions of individual cells without changing the vertical and horizontal directions of cell axes were observed relatively frequently, as seen in Nests 8 (Fig. 42), 220, 331 (Fig. 21) and 399 (Fig. 24).

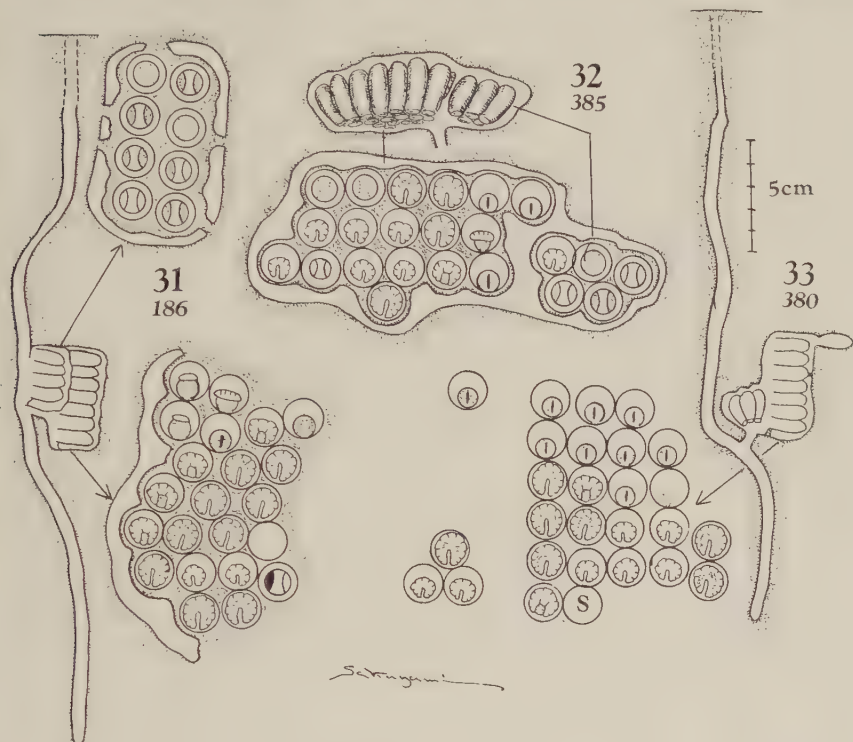
Abnormal orientations in the horizontal plane: a. Cell taking position perpendicular to *C*: 175 (Fig. 22), 357, 361 (Fig. 23, 25), 381 (Fig. 26), and in an extremely complicated manner 391 (Fig. 30). b. Cells partly taking the diametrically opposed direction to that of *C*: 370 (Fig. 27).

Very abnormal orientations: Cell almost *erect* (Fig. 23) or *invert* (Figs. 28, 29).

e) *Occurrence of two CC in a common cavity.*—This must not be confused with the two cavity nests touched upon later in 2.6, although both are seemingly causally related. In the present case, two *CC* occur within the

same *Ca*, without having contact with each other. This arrangement was found in Nests 186, 385, and 380 (Figs. 31-33). In the last mentioned nest, which illustrates also the abnormal right angular orientation of one *C*, three isolated *CC* were found, two in the cavity and the third as yet (consisting of only one cell) in the wall of cavity.

It cannot be determined whether these departures from the standard



FIGS. 31-33. — Nests with two separate clusters within one and the same cavity. *S* in the Fig. 34 means the emergence of a cuckoo bee, *Sphecodes*.

plan mean either any adjustments or only mere misbuildings, or are the outcome of behavioral atavism. At any rate, they show the fairly variable nature of the apparently uniform architectural plan of this species. The most abnormally oriented cells described above in *d*) were those which constructed after the completion of the main cluster body, as shown by they containing in most cases relatively younger immature stages than those within the cluster proper (Figs. 20, 22, 23, 25, 27, 29, 33).

1. 4. Cavities (*Ca*) around clusters.

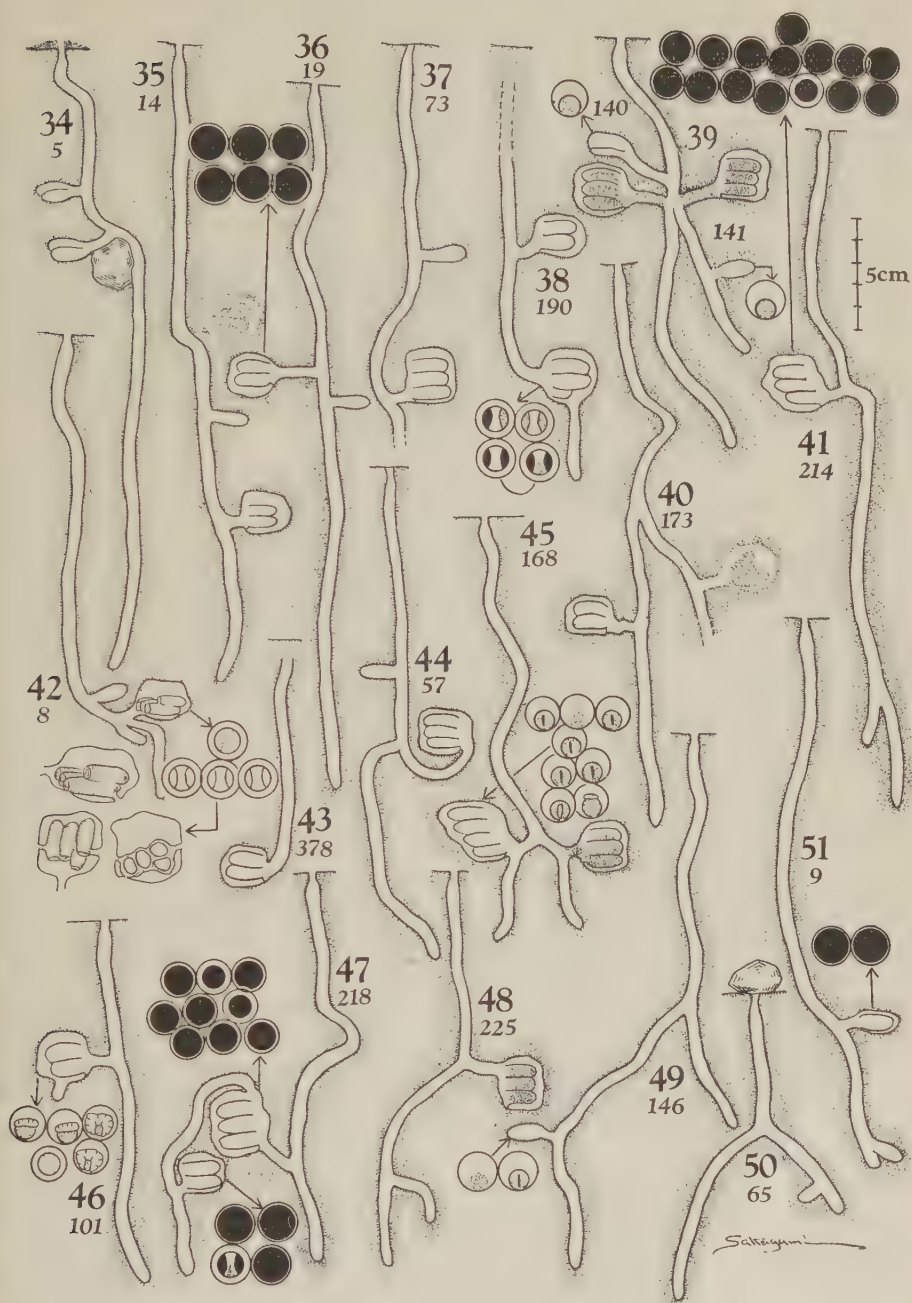
The occurrence of an empty space around *C* is also a characteristic feature of the nest of this species (Cf. Figs. 1, 130). The cavity, *Ca*, is still incomplete or absent in the younger nests containing a few cells.

In the advanced nests, however, the soil surrounding *C* is almost completely removed (with exceptions described in 2.4.), leaving several earthen pillars which support *C* within *Ca*. In such nests, the wall of cavity is fairly smooth. The distance between the cavity wall and *C* is variable but usually sufficiently wide to permit the free movement of inhabitants, rarely wider than the size of *C* as in Nest 8 (Fig. 42). The numbers and positions of pillars are also variable. The upper, lateral and posterior pillars are frequently observed in younger nests, but rather exceptional in advanced nests (Figs. 33, 42). In such nests, *C* is attached to the cavity wall only at the anterior bottom, either by a few large pillars or by several finer ones (Fig. 15). The interspaces between the pillars are, seemingly, used by the inhabitants as a passway. Moreover, a passway penetrating the center of *C* was found in Nests 382 and 381 (Figs. 17 and 26, *P*). Judging from the smooth walls of these passways, it is clear that they were secondarily modified from a brood cell. On the other hand, the narrow intercellular passways found in Nests 345 and 391 (Fig. 30, *P*) are apparently of a primary construction perforated in the soil mass between two cells. The opposite case, the unutilized remnants of a soil mass between cells were seen in two nests, 345 and 396 (Figs. 91 and 92), indicating the occasional lack of spatial economy, a relatively infrequent phenomenon in this species.

1. 5. Additional notes on some abnormal structures.

It is needless to describe the last nest element, *L*, in this section, for it is practically an extension of *U*. Instead, some abnormal nest structures are here briefly touched upon as the final part of Section I, because their deformities could not be appropriately described within any of above sections.

1. 5. 1. Extra lateral burrow.—A short lateral blind burrow was found in the following nests: 8, 14, 19, 57, 73 (Figs. 35, 36, 37, 42, 44). As the last two were not spring nests, but old summer ones made in the previous year (1956), all such blind burrows were found in summer nests. In every case, the branch does not exceed 20 mm in length and is about as wide as *U* in diameter, with the inner wall not specially elaborated. Blind burrows were found both above and below *Ca* in Nest 8, below *Ca* in 19, and above in other three cases. Judging from their relation to *Ca*, and the comparison between these nests and others, especially those with two cavities, it seems to be inappropriate to consider them as abnormal structures, at least in those which possess the extra lateral below *Ca*, because these perhaps represent not an abnormal structure, but merely unfinished two-cavity nests. Thus these blind laterals might be the abandoned first *H* (if they occur above *Ca*) or second *H* (if below *Ca*),



FIGS. 34-51. — Variability in main gallery.

of which further elaboration was interrupted before or after the construction of *Ca*.

1. 5. 2. Nests with abnormal lower shaft.—The occurrence of an unramified vertical lower shaft is a specific character of the nest of *H. duplex*, and of many other allied species, but the following abnormalities were discovered in certain nests.

a) *Nests devoid of L*.—Although the lack of *L* in younger nests still with only a few cells may not be regarded as abnormal (Figs. 65, 66, 121, 126), the absence of this element was noticed in two nests which were already in fairly advanced stages: 4 and 378 (Fig. 43). *L* was absent also in nests 174 (Fig. 124), 195, 340 (Fig. 126), 339 (Fig. 73), 343, 355 but it is uncertain whether these ought to be regarded as abnormal cases or as young nests in which *L* was not yet constructed.

b) *Abnormal origin of L*.—In Nest 101 (Fig. 46), *L* was normal but another short vertical shaft issued from the bottom of *Ca*. In nest 190 (Fig. 38), a vertical burrow descended from the bottom of *Ca* and the normal *L* was wanting. As a still more curious case, Nest 218 (Fig. 47) possessed, besides the normal *L*, another shaft issuing from the top of *Ca*. This ran first horizontally, then vertically along *Ca*, and gave rise to the second *H* (connecting with *Ca*₂) at the middle of its vertical portion. From these nests, it is evident that the point at which *L* issues is fairly well fixed but not always absolutely so in *H. duplex*.

c) *Branched L*.—Nests with branched lower burrows can be subdivided into three groups: 1. Those in which a new *L* was constructed in summer, while the old *L* made in spring remains unutilized (Nests 146, 168, 173; Figs. 49, 45, 40). In 146 the spring cavity was already obscure, in the other two nests, the depths of spring and summer cavities seldom differ. 2. Those with each leading to a summer *Ca* (Nest 338, Fig. 120). It is interesting that this is the unique nest with three-cavities among hundreds examined. 3. Those with a slight bifurcation of the lowest part of *L*. This was found in Nests 9, 214, 225 (Figs. 51, 41, 48). These nests were found altogether after the cessation of summer activity. Hence, it is highly probable that this bifurcation means not an abnormal construction but the formation of hibernacula independently executed by wintering females.

It may be noteworthy to cite an instance of abnormal branching induced artificially (Nest 65, Fig. 50). On May 8, 1957, the nest owner was observed when returning to the nest. Another female was artificially put into the nest after marked with color-paint and the entrance was firmly closed with stone. The nest was excavated on May 16 and the double branching was discovered. The first bifurcation may represent the independent activities of two females forced to co-exist, but the second one indicates the appearance of abnormal behaviour under the adverse condition.

1. 5. 3. Communal entrance.—From the purely morphological standpoint, such entrances may be discussed under branched shafts, the branching point being located near the soil surface. The significance of communal entrances is far more important. The use of a common entrance by two independent nest owners has been repeatedly described with the bees forming *composite nests* including various halictine species. In spite of the strong tendency to form a dense colony (*pseudocolony* of Malyshev), such the communal use of an entrance is extremely rare in *H. duplex*. Two nests can often stand very closely, say 1 cm for each other. But, internal connections between them were never found. The communal entrance was found only in one instance: Nest 140 and 141 (Fig. 39). In this case, two nests were seemingly independent for each other in spring period. The common entrance in summer period was perhaps caused accidentally due to the short distance between the two nests.

II. — NEST CONSTRUCTION

Except for the initial phase of burrowing, the major parts of nest construction are performed under the soil surface hidden from the eyes of observers. Consequently, the process of construction must be reasoned by comparing nests showing various stages of development. Therefore, it may be legitimate to mention here that the following description might include false interpretations inevitably caused by the lack of appropriate observations.

2. 1. Burrowing behaviour.

The burrowing behaviour of *H. duplex* scarcely differs from that found in other digger bees. The bees begin their activity usually after a considerable period spent for nest site selection. At first they dig capriciously and often abandon the site because of insignificant stimuli or even spontaneously. After the thorax is inserted the soil, however, they become eagerly and the digging speed markedly increases. At this phase, they can be easily marked with color-paint without disturbing their performance. It was also occasionally observed that the bees were indifferent to troublesome antennal interference by the workers of *Formica fusca japonica* Motschulsky.

The chief digging tools are mandibles and fore-legs. These are used approximately synchronously, but each of forelegs moves, in the strict sense, neither synchronously nor alternatively. The mandibles throw the excavated soil particles backward, while the fore legs throw them slightly obliquely. The middle legs occasionally participate in the digging act but are mainly stretched, together with hind legs, against the soil to support the balance of body (Fig. 53). Throughout the digging activity,

the body frequently rotates around the axis of the burrow (Fig. 54). After the anterior half of abdomen becomes invisible under the soil surface, an alternation of digging and pushing the soil mass rhythmically appears. Because of the pushing action of mandibles and fore legs, the soil accumulates behind the body. Then, the bees begin a backward movement and push out the soil mass by means of the hind legs and abdomen (Laboratory observation through the glass window).

The speed of digging varies naturally according to the soil texture, and was quite rapid in the loose soil of University Botanical Garden. Thus, the duration from the beginning of digging to the disappearance of the apex of the abdomen in the burrow was, in some instances, 28', 15', 15', 14', 8', 8', 5', 5', respectively. The chief cause of variability is the frequent interruption of activity at the initial phase. If the activity is continued without such interruption, the body disappears under the soil within 5-10'. This process may be visualized from Fig. 52, which was drawn from an observation taken on April 30, 1958.

2. 2. First *H*, then *L*, or vice versa ?

Before the construction of *H* and *C*, the nests are nothing more than simple vertical burrows with the entrance constrictions (Figs. 5, 55-63). The constriction is already found in the youngest nests such as 74 (Depth 2.5 cm, Fig. 56), or 239 (3 cm, Fig. 55). After *U* reaches a sufficient depth,

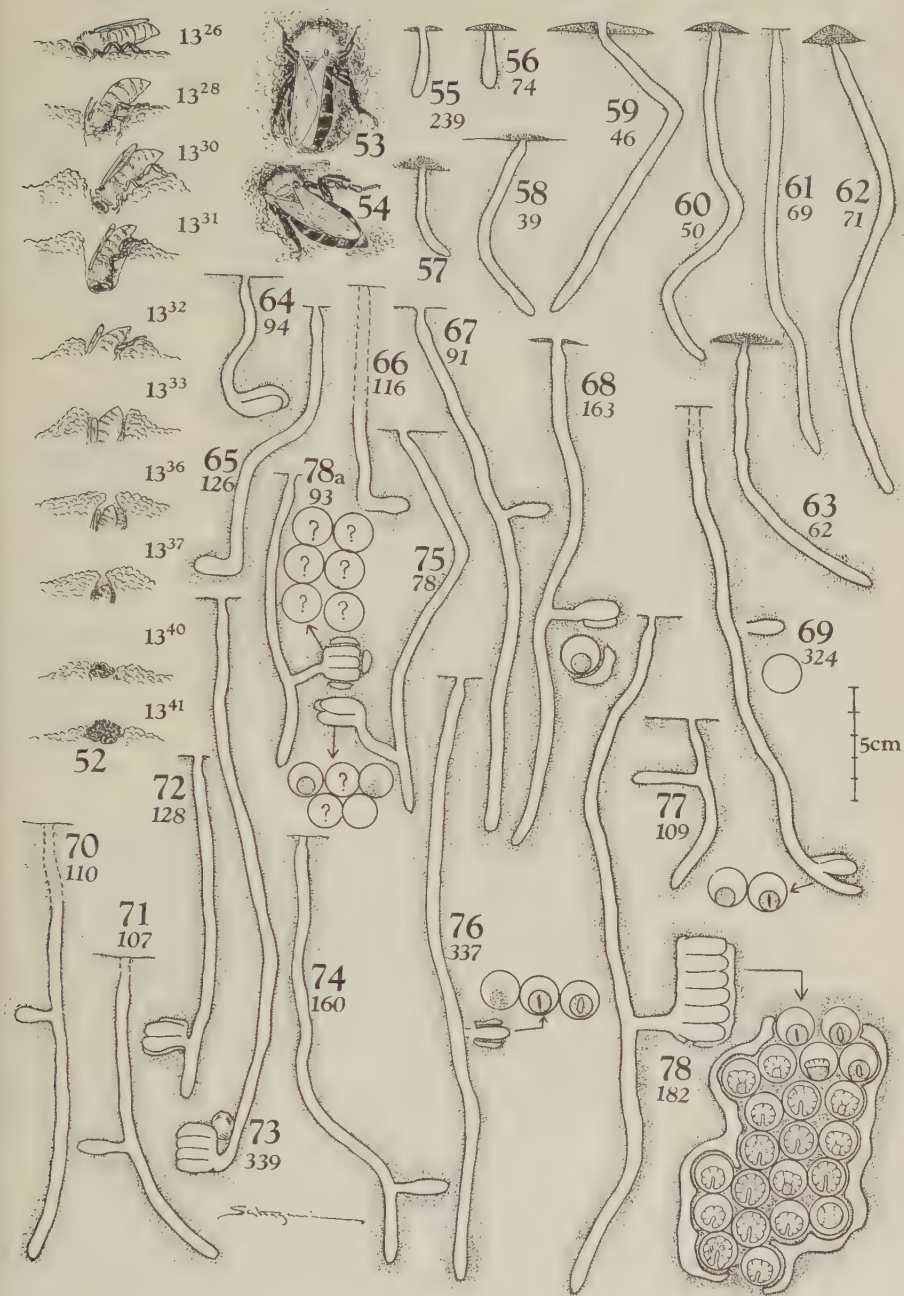
TABLE 9. — FREQUENCY DISTRIBUTION OF THE DEPTHS OF *H* AND *L* IN SPRING NESTS.

DEPTH (cm).	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	19	20	21
<i>H</i>	1	1	2	2	2	5	4	4	8	3	9	5	4	5	1	1	1		1
<i>L</i> (*)		4	1	3	9	13	13	14	6	4	5	1	2	1					

(*) Depth of the end of *L* in the nests still without *H* and *C*.

the construction of *H* commences. It is clear that *H* is made before *L*, at least in certain instances, because there were found nests with *H* but still devoid of *L* as follows: 94, 331, 332 (with only one cell, without or with incomplete *Ca*, Figs. 64, 121), 116, 126 (with only one half-built cell, without *Ca*, Figs. 66, 65). On the other hand, it is difficult to conclude that *H* is *always* made before *L*, because of the indirect evidence mentioned below.

In Table 9, the depth of *H* in spring nests and that of the burrow and in younger spring nests which still lack *H* and *C* are synoptically presented.



FIGS. 52-78. — Nesting behaviour and nests of incipient stages.

As the distribution of the depths of burrows includes even the data taken from the nests of the youngest stage, it does not represent the depth of nests still without *H* and *C*. Nevertheless, there are found numerous cases in which the burrow end is much deeper than the mean depth of *H*. This may suggest the probable construction of *H* after the latter was already dug out to a considerable depth. Perhaps *H* may be made either before or after the deepening of *L*, and both may be further lengthened simultaneously. This is assumed also from the relative depth of the end of *L* in nests at various developmental stages. According to the stages, nests were classified as shown below, and the relationships between nest stages and the depth of the bottom of the burrow relative to the cavity depth were summarized in Table 10.

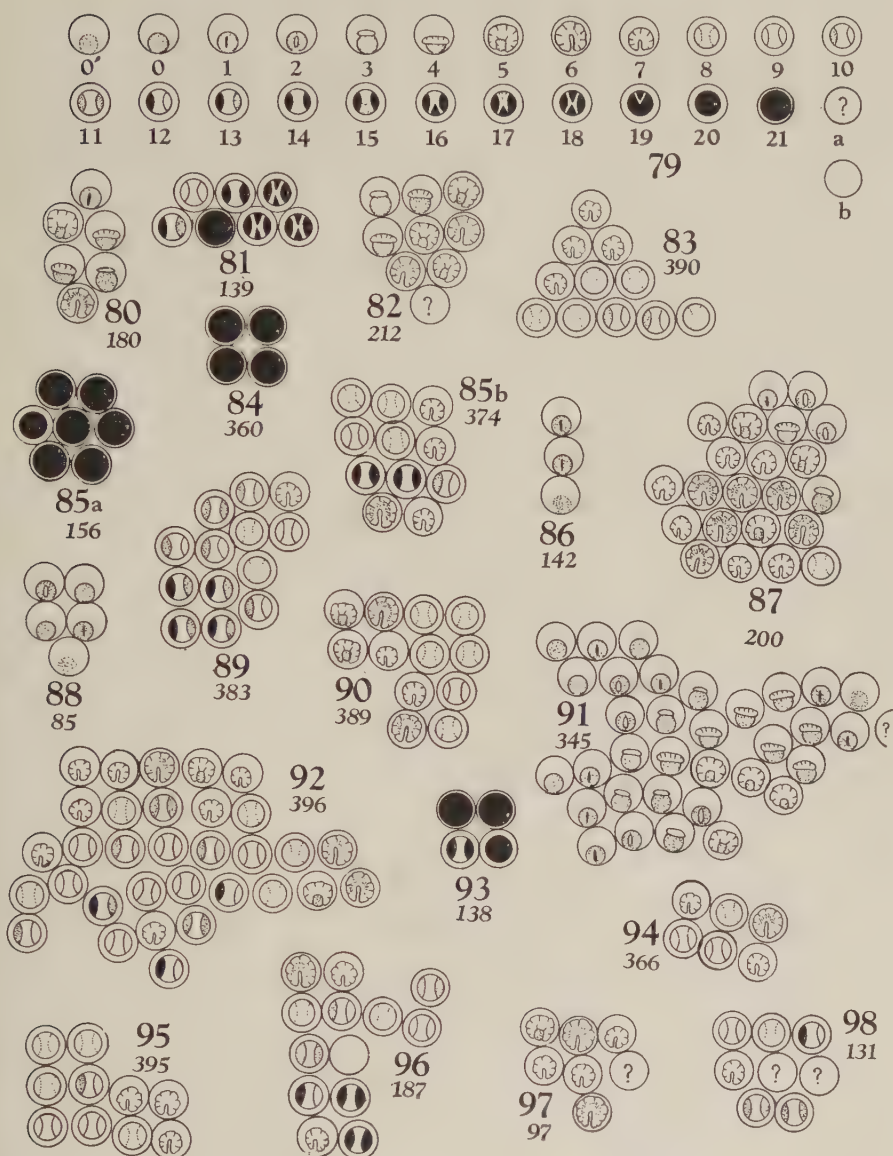
- A : Nest still without complete *Ca*.
 B : Nests still with eggs.
 C : Nests already without eggs.
 D : Nests already without unpigmented pupae.
 E : Nests in which all progeny emerged.

TABLE 10. — DISTANCE BETWEEN CAVITY BOTTOM AND BURROW END (shown by vertical distance, cm) (1).

DISTANCE.		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	23	25
NEST STAGES (**)	A	7	1	3	5	1	2	3	1	2		4	4										
	B	2	2	4	2	3	3	2		3	2	2	3			1							
	C	1	1	4	7	3	4	7	2	2	1	2	1		1								
	D					1		2		1	1	2	2							2	1		
	E			1	2		4		2		1	4	1	1	1		1	1	1			2	1

(*) Spring and summer nests combined, as no significant difference exists between them.
 (**) Cf. in text.

Two facts are obvious from the table: 1) There occurs a general tendency for the gradual deepening of the burrow parallel with the development of immature stages, but 2) only with a fairly large magnitude of variability. This suggests the lack of strictly predetermined temporal sequence in constructing *C* (or *Ca*) and *L*. Hence, the nest of this species can be regarded as belonging to the *dispersed type* of MALYSHEV, because of the absence of a definite relation between deepening of the burrow and increase of cell number, although his type was primarily proposed for the non-comb builders.



FIGS. 79. — Schematic representation of developmental stages (a: undetermined, b: empty. On other figures see in Section 2. 3. of text). FIGS. 80-98. — Various developmental gradient within the cluster.

2. 3. Arrangement of brood cells within *C*.

As in the cases of other Aculeata, the temporal order of cell construction in *H. duplex* can be estimated from the degree of development of immature stages contained in each nest. From the data given in Sec. III, the following stages were distinguished in order to recognize the developmental gradient within *C* (Cf. Also Fig. 79):

- | | |
|---|---|
| 0': Pollen mass still not shaped. | 11: Yellow pupa with orange eyes. |
| 0: Pollen ball alone. | 12: Yellow pupa with pale violet eyes. |
| 1: Eggs (Fig. 132). | 13: Yellow pupa with violet eyes. |
| 2: First instar larva (Fig. 133). | 14: Yellow pupa with black eyes. |
| 3: Second instar larva (Fig. 134). | 15: Pupa with thorax and abdomen slightly pigmented. |
| 4: Third instar larva (Fig. 135). | 16: Pupa with much advanced pigmentation. |
| 5: Forth instar larva with pollen ball (Figs. 136 and 137). | 17: Pupa with head and thorax entirely black. |
| 6: Pre-defecation forth instar larva without pollen (Fig. 138). | 18: Black pupa, only tips of antennae and legs white. |
| 7: Post-defecation larva (= Prepupa, Fig. 139). | 19: Pupa entirely black. |
| 8: White pupa (Fig. 140). | 20: Adult within cell. |
| 9: Yellow pupa. | 21: Cell after emergence. |
| 10: Yellow pupa with eyes slightly pigmented. | |

Among all the nests excavated during 1956-8, the developmental gradient was relatively well traced in 84 clusters. The frequency distribution of *CC* showing variously developmental gradients are presented in Table 11. The upward gradient obviously dominates the majority

TABLE 11. — FREQUENCY OF CELL CLUSTERS SHOWING VARIOUS DEVELOPMENTAL GRADIENTS.

TYPE OF GRADIENT.	FREQUENCY.	EXAMPLES (Number of Text-figures).
Distinctly upwards (*)	46 54.4 %	15, 17, 26, 78, 83, 116, 127.
Approximately upwards.....	8 9.6 %	13, 31, 80, 81, 82
Approximately upwards, with a slight lateral gradient	11 13.2 %	16, 85 b, 89, 90, 92
Slightly downwards	5 6.0 %	88, 93
Lateral.....	2 2.4 %	95, 105
Upwards, with a slight downwards gradient	2 2.4 %	96, 119
Irregular	10 12.0 %	29, 30, 32, 87, 91, 94, 98, 115

(*) Including nests with later addition of cells as seen in Figs. 22, 23, 25, 29.

of *CC* examined. This is especially true in larger *CC* in which the developmental gradient can be distinctly traced. The lateral gradient was occasionally found in combination with the upward one. On the other hand, all five *CC* showing a slight downward gradient were relatively small ones. Consequently, it is concluded that the cells were gradually added upwards. This coincides well with the fact that *H* usually opens at the lower half of *Ca* as mentioned in 1.2, suggesting the simultaneous upward enlargement of both *C* and *Ca*.

2. 4. Completion of *Ca* and simultaneous execution of several activities.

The manner of *Ca* formation around *C* is best assumed by examining the nests still with half-built *Ca*. Among all the nests examined, however, such ones were relatively scarce, only 14 younger nests and 7 advanced ones being appropriate for this study. With respect to these nests, the surroundings of *C* were classified into six sections, front, back, sides, top and bottom of *C*, and the completion of *Ca* under these headings was explained in Table 12. The data taken from younger nests give a suggestion on the section from which *Ca* construction is commenced. Those taken from advanced nests, on the other hand, show which section is frequently untouched. It is evident that *Ca* is commenced from the front. As to other sections, back, bottom and sides are seemingly excavated rather synchronously, but the top section shows a definite delay of excavation. This accords well to the upward developmental gradient of *C* formation mentioned in the previous section, because *Ca* construction at the top section may set a limit to the further development of *C*. (1) The complete excavation of the top section was found in only two of the 21 nests, one of which is an abandoned spring nest, 94 (Fig. 64).

The back section of *Ca* is often untouched in younger stages, but almost completed in advanced ones. Besides the partial development of *Ca*, another type of incompleteness was occasionally observed as in nests 343, 344. In them, *Ca* was already well outlined around *C*, but the space between *C* and *Ca* walls was still very narrow, with much loose soil just excavated. Consequently, the formation of *Ca*, although fairly variable from nest to nest, generally commences from the front and bottom of *C*, and proceeds upwards parallel with the development of *C*.

This simultaneous development of *Ca* and *C* is shown in Table 13. The

(1) This assumption postulates the absence of cell formation within excavated cavity as in some pot-making Aculeata. If *H. duplex* behaves as the pot-maker, not only the above assumption but also results on the cell number per nest given in 1. 3. 2. will have to be reconsidered, for the occurrence of complete *Ca*, then, would not always mean the end of *C* development. However, judging from the habits of this and allied species, the occurrence of pot-making is not highly probable. The opinion of Prof. CH. D. MICHENER (in personal communication) accords with writers' on this point, although pot-making by certain American halictine species was suggested by MICHENER et LANGE (1958, a, b).

TABLE 12. — ADVANCEMENT OF *Ca* FORMATION AROUND *C* (*).

NEST No.		FIG. No.	<i>Ca</i> IS COMPLETED (+) OR HALF-BUILT (±) AT <i>C'</i> c.				
			Front.	Sides.	Back.	Bottom.	Top.
Nests of younger stages.	94	64	+		±		+
	140	39	+			+	
	142	100	+	+	±	±	
	145	114	+		+	+	
	149	113	+			+	
	161	102	+	+	+		
	163	68	+	+		±	
	176	107	+		+	+	
	179	117	+	±			±
	335	101	+	+		±	±
	337	76	+	±		±	±
	338	120	+		+		
	»	»	+	+	±		
	»	»	+	+	+	±	
Total.			14	5.7	5	6.5	3
Nests of advanced stages.	167	103	+	±	±		+
	182	78	+	+	+		
	186	31	+		+		
	201	109	+	+	+		+
	206	—	+	+	+	±	±
	211	104	+	+	+	+	
	341	105	+	+	+	+	±
Total.			7	4	7	2.5	3

(*) Absence of a symbol indicates that *Ca* has not been formed in that position.TABLE 13. — RELATIONSHIP BETWEEN FORMATION OF *Ca* AND *C* (*).

TOTAL CELL NUMBER.	NEST WITHOUT <i>Ca</i> .	NEST WITH HALF-BUILT <i>Ca</i> .	NEST WITH COMPLETE <i>Ca</i> .
1	17	2	2
2	3	2	1
3	3	3	13
4	1	3	26
5		1	27

(*) Advanced nest with half-built *Ca* are excluded (Cf. Table 12).

youngest nests with only one cell are still mostly devoid of *Ca*. But the nests with more than 3 cells mostly possess a more or less developed cavity. This naturally does not mean that *Ca* formation is complete at this stage in every nest. If such were the case, it hardly seems possible that nests with more than 3 cells would actually develop. The table suggests merely that *Ca* formation begins usually after one or two cells are constructed and proceeds thereafter, often rapidly parallel with the development of *C*.

Another aspect of simultaneous performance may be cited here. As in many solitary bees, females of *H. duplex* complete each brood cell in the following order: Cell construction—Foraging and food deposition—Formation of Pollen ball—Oviposition—Cell closing. Therefore, if one nest contains more than one open cell, still empty or provided with food alone, it may prove the simultaneous care of these cells by the nest owner or owners. Table 14 shows such is often the case. Thus at least 4 (in the

TABLE 14. — OCCURRENCE OF MORE THAN ONE CELL BEFORE OVIPOSITION WITHIN ONE NEST.

CELLS BEFORE OVIPOSITION.				NUMBER OF NESTS.			EXAMPLES (Fig. No.).
Empty.	Pollen before manipulation.	Pollen ball.	Total.	Spring.	Summer.	Total.	
	2	2	4	1		1	
		2	2	1	5	6	
		3	3		1	1	25
	1	1	2		2	2	12
	3		3		1	1	103
	1	2	3	1		1	88
	1	2	3		2	2	
	2		2		2	2	117
2			2		1	1	
2		2	4		1	1	
1		1	2		1	1	126
1	1		2		1	1	
	1	4	5		1	1	91
			Total.	3	18	21	

spring solitary phase) or 5 cells (in summer gregarious phase) can be cared simultaneously before completion of any of them. Three examples taken from spring nests are especially important, for they reveal the simultaneous work can be performed by the single nest mother in the spring solitary phase. On the other hand, the clear explanation of all other cases taken from summer nests is more difficult because of the occurrence of more than one inhabitant in this period.

However, there is no evidence of the complete synchronous construction of many cells such as in honeybee. The construction of one cell seems to

be started at least after the lining of the precedent one was finished. Hence, the cell construction of this species belong to *serial, semi-honeycomb type* of Malyshev.

Anyhow, it was clarified from the above description that this species can simultaneously perform various tasks such as deepening of the lower shaft, construction of brood cells and the cell cavity, foraging, preparation of pollen balls and closing of cells after oviposition. This tendency, being reported also in other halictine species, but rather rarely in other solitary bees and wasps, was suggested by Legewie (1925) and Weyrauch (1939) as the commencement of behavioural plasticity making possible the gregarious life, although such habit is found in a true solitary wasp, *Ammophila campestris* Jurine (Baerends, 1941).

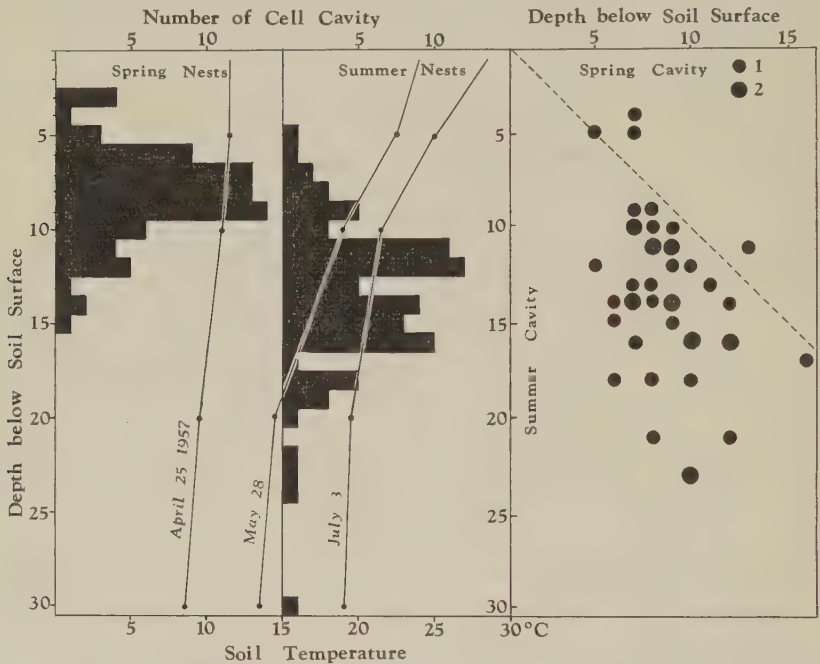
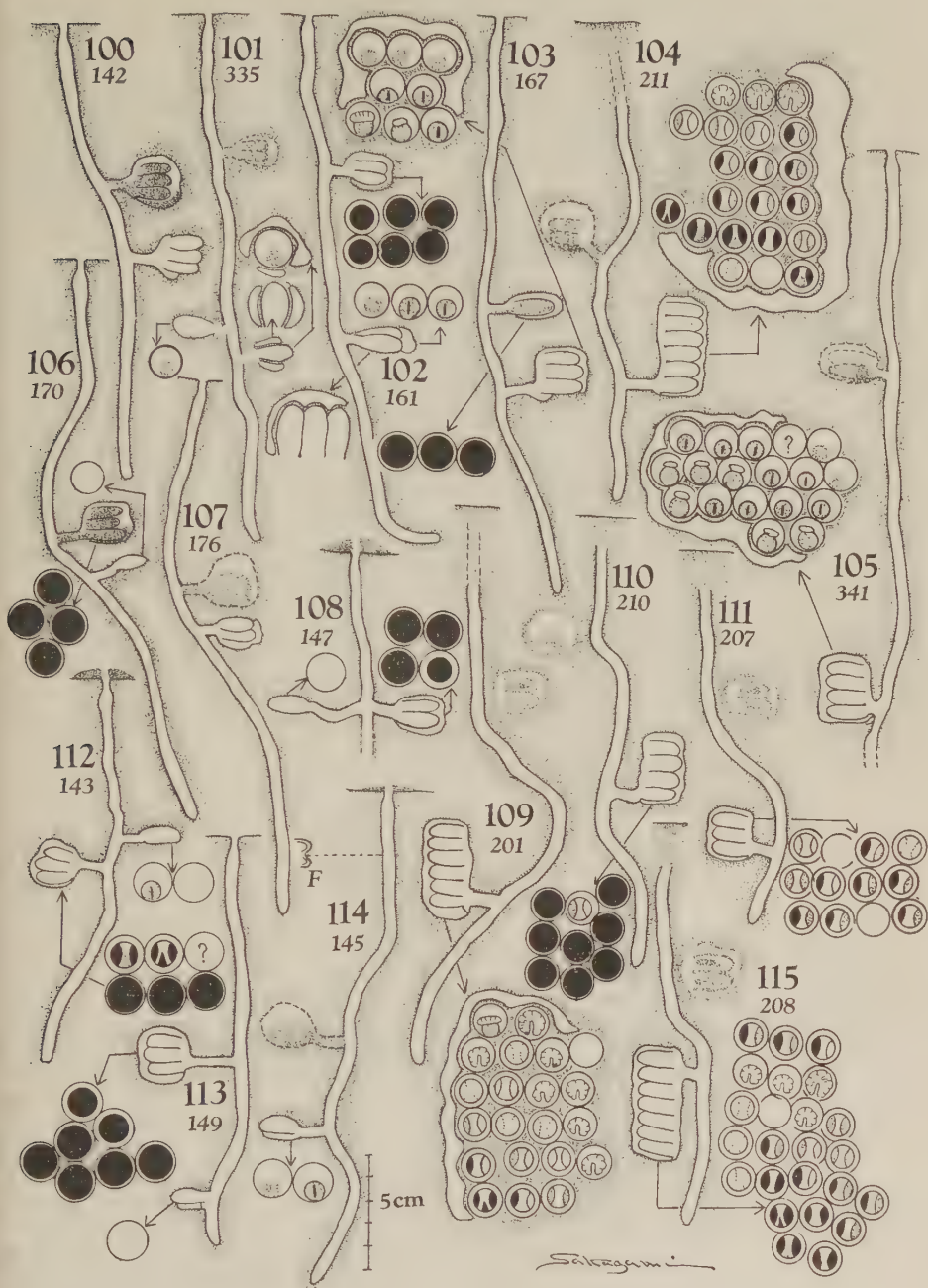


FIG. 99. — Vertical distribution of cell-clusters in 1957. Left: Thermal gradient and difference of cluster distribution between spring and summer nests. Right: Relative depth of spring and summer cluster within the same nest.

2. 5. From spring to summer nests.

Here is given additional information regarding the relative depth of spring and summer CC. The construction of summer CC deeper than spring ones may correlate with the vertical thermal and hygroscopic gradient of the soil. In 1957, occasional measurements were taken of the soil temperature and water content at various depths below surface. The data on water content were discarded because of their extreme variability



FIGS. 100-115. — Summer nests with more or less detectable spring cavities. *F* in Fig. 114 represents the corner of the nest of the ant, *Formica fusca japonica* Motschulsky, located 3 cm apart from the main gallery.

according to the rainfall preceding the measurement; nevertheless this factor is supposed to be as important as thermal conditions. In fig. 99 left, the vertical distribution of both spring and summer *CC* are illustrated, accompanied by the thermal gradient in three successive observations, all taken in fair weather at approximately 15⁰⁰. As seen in the figure, the thermal gradient was more conspicuous in summer than in spring just at the depth where a concentration of spring *CC* was observed, suggesting the influence of thermal condition upon the relative depth of *CC* distribution.

As already reported in the previous paper, the spring *Ca* are often more or less distinctly visible even after the summer *Ca* are being constructed. Based upon the examination of these nests, Fig. 99 right shows the relative depths of both clusters in one and the same nest. If summer nests contain more than one *Ca*, each was regarded as an independent case. The deeper position of summer *CC* is obvious from the figure, the reversed instances were found only thrice; Nest 140 (39), 174 (124), 198 (123). On the other hand, there is no clear correlation between absolute depths of both *CC* in one and the same nest.

The relation of cell number in spring and summer *CC* within the same nest was also examined. But the most of summer nests in which the spring *C* was detected still possessed only a half built *Ca*, or cells contained eggs or pollen masses alone, suggesting the further development of *C*. Excluding such ones, the following cases were obtained:

CELL NUMBER		
in Spring	and	in Summer CC.
3		5, 8, 9
4		18, 20, 21
5		5, 13
6		12, 13
7		8

Owing to the lack of sufficient material, no definite conclusion can be reached. But the lack of strict proportionality between two periods is conceivable also from the fact that all the daughters do not necessarily remain in the mother's nest in the summer.

The summer *CC* are occasionally commenced before the emergence of all the spring broods. The overlap of broods of two periods were observed in the following 4 nests (Developmental stages are shown by the numbers given in 2.3 and Fig. 79).

NEST No.	(Fig. No.)	SPRING C.	SUMMER C.
143		15-21	empty-1
147		20-21	—
149	(113)	20-21	a half built cell
161	(102)	20-21	0'

Therefore, here is another aspect of simultaneous performance of two tasks, the construction of a new *C* and filling up of the old *C* by soil gradually proceeds in parallel to the emergence of the broods. At first each cell, then *Ca* itself, finally *H* is worked out. Filling up of *Ca* is relatively loose, but of *H* is often so compact that the spring *C* is difficult to trace.

2. 6. Nests with two cavities.

Throughout the above description, the occurrence of nests with two cavities were repeatedly mentioned. Two-*Ca* nests are, although found exclusively in summer period, not always a rare event (1). The proportion of them to the total nests excavated was 11.4% (10/88) in 1957 and 13.7%

TABLE 15. — CHARACTERISTICS OF NESTS WITH TWO SUMMER CAVITIES.

DATE.	NEST No. (Fig. No.).	HEIGHT OF <i>H</i> (cm)			CELL NUMBER				YOUNGEST & OLDEST IMMATURE STAGES (*)		TOTAL NUMBER OF ADULT FEMALES.
		P	C ₁	C ₂	P	C ₁	C ₂	C ₁ + C ₂	C ₁	C ₂	
VII 18	172 (122)	9	12	19	?	10	6	16	0-3	0'-0	4 1 (**)
	24 174 (124)	13	11	18	5	1	8	9	3	0'-3	6
	179 (117)	8	9	18	6	3	2	5	0-2	0'-0'	3
	31 189 (119)	?	13	19	?	3	18	21	8-11	2-7	1 1 (**)
VIII 7	191 (125)	11	13	17	?	10	6	16	11-15	6-8	1
	198 (123)	6	5	12	?	4	6	10	10-11	4-8	—
	202 (116)	5	9	14	9	3	19	22	13-13	7-12	2
	14 209 (118)	7	13	14	6	5	8	13	14-15	14-16	2
	218 (47)	?	12	14	?	9	4	13	20-21	15-21	2
	220 (127)	?	11	15	?	4	1	5	21-21	8-21	0 1 (**)
VII 12	324 —	?	10	20	?	1	1	2	empty	0-1	0
	332 (121)	8	13	21	?	3	1	4	0	0	2
	334 (128)	?	?	?	?	5	5	10	0-1	0-1	2
	335 —	6	14	15	3-4	1	1	2	0'	0'	—
	340 (126)	?	?	?	?	3	11	14	4-5 (***)	0'-4 (***)	—
	360 —	?	21	24	?	13	17	30	5-9	1-6	3
	362 —	?	15	21	?	5	13	18	8-9	0-8	—
	395 —	?	16	21	?	10	7	17	7-10	5-6	—
	397 —	?	15	22	?	29	25	54	6-13	5-9	1 1 (**)
	398 —	?	15	21	?	2	27	29	13-13	6-13	—

(*) Stages given in 2. 3. (Fig. 79).

(**) Dead females found in nests.

(***) Excluding empty cells before deposition of pollen.

C₁, C₂: First and second summer cavities (or clusters). The cavity in the less deep position is called the first cavity (C₁).

P: Old spring cavity or cluster.

(1) According to Mr. HIRASHIMA, *Halictus affinis* Smith, which is a close relative of *duplex* and makes nest very similar to those of the latter species, constructs mostly two *Ca* in summer in Fukuoka, Kyushu (personal communication).

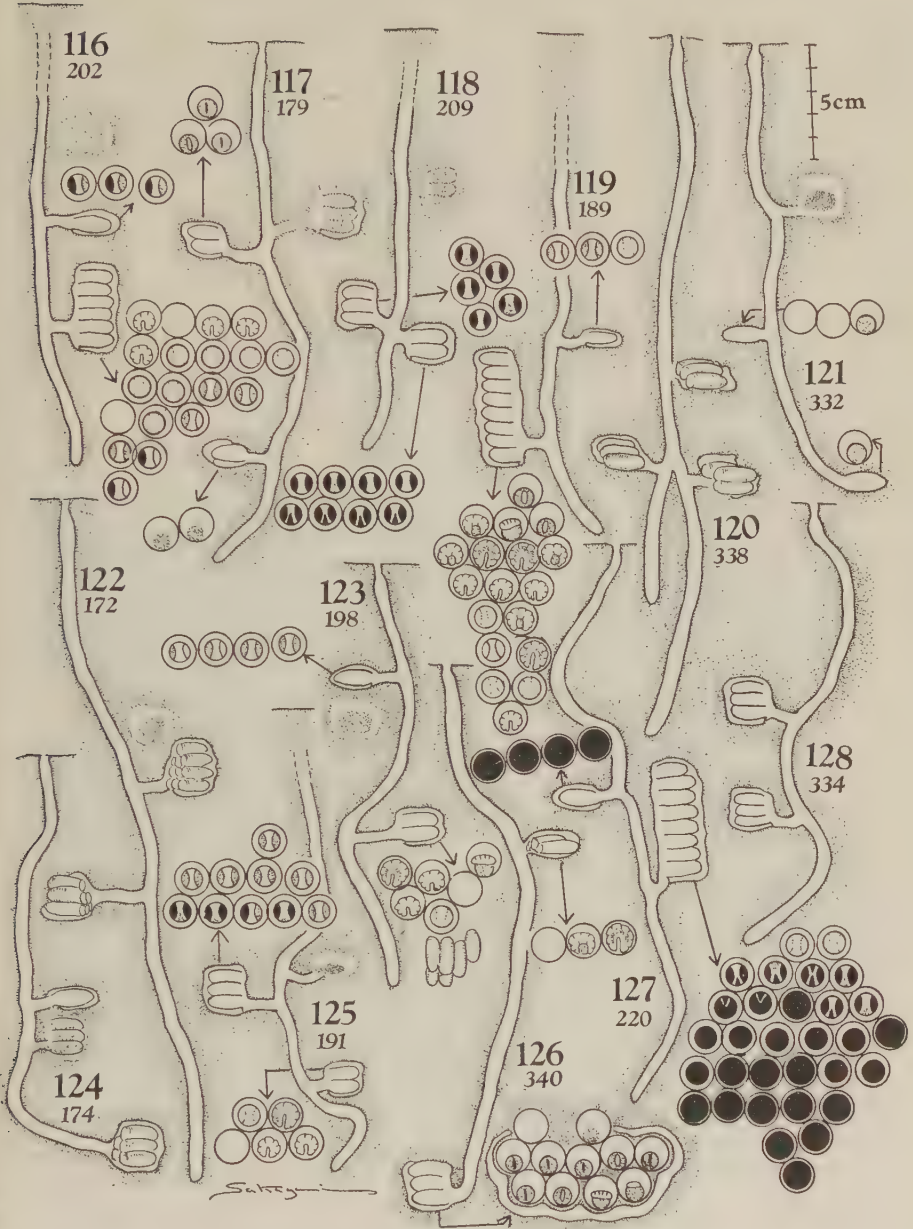
(10/73) in 1958. The data on these nests are shown in Table 15 and Figs. 116-128, from which the following facts are established: 1) The relative depths of the two cavities varies from nest to nest, but mostly one is distinctly deeper than the other, and for both cavities, deeper in 1958 than in 1957, perhaps because of adverse soil conditions suggested in 1. 2. 2) The relative sizes of two *CC* is also variable. The first *C* was larger in 8 nests, smaller in 9 nests, and as large as the second in 3 cases. But, marked differences was usually found in the nests in which the second *C* is the larger. 3) If the cell numbers of both *CC* are combined, the total cell number is often very large in two-*Ca* nests in comparison with that of single-*Ca* nests. 4) Except for Nests 324, 335, which were still in very incipient stages, the second or lower *Ca* contained younger immature stages than the first one, suggesting later construction of the lower one. 5) An overlap of stages between the two clusters was found in 13 nests, but was absent or obscure in the other 8, indicating that the cavities may be cared for either successively, or at least temporarily, simultaneously.

It is not easy to find an adequate explanation of the question of why some summer nests of this species possess one and other *Ca*. The following three assumptions are probable but still cannot be sufficiently proved by the concrete evidence. 1) After the construction of the first summer *Ca*, the bees perceive the adverse thermal and hygroscopic conditions and behave adjustively. This assumption is partly supported by the comparison of depths of *Ca* in two and one *Ca* nests. The difference is, however, not always distinct. Moreover, there is no clear difference in the relative mortality of immature stages between the first and second *Ca*. Perhaps some nests in which the first *Ca* is relatively shallow and contains only a few cells may be explained by this assumption. 2) When there are more than one females per nest, each female tends to behave independently from her nest mates, which results the construction of the second cavity by one or more females while the first one is being cared for by other nest-mates (1). 3) If there are many inhabitants, the construction of *C* and *Ca* proceeds rapidly up to the average cell number of summer clusters. The excess ability for construction is, consequently, expressed by the formation of the second cavity.

The causes of two-*Ca* nests is not clear at present and must be sought in further investigation. In contrast to the old spring *Ca*, the first summer *Ca* is not filled up even after the emergence of all the brood in it.

Finally the unique case of a three *Ca* nest, Nest 338 is discussed here. This nest is also remarkable for the occurrence of two lower shafts (*Cf.* 1. 5.2. *c*, Fig. 120). Thus, two lower *Ca* are constructed each along an independent *L*. The location and contents of each *Ca* are:

(1) This does not mean the independent care for each cell by each nest mate as suggested by APTEL (1931) in *H. malachurus*. Such may be hardly probable from the structure of nest in *H. duplex*. Claude-Joseph suggested the independent care of each cell by cohabitants even in the comb-builders of Chilean halictine bees. But the writers possess evidence of communal care for one cell by several females as will be described in another paper.



FIGS. 116-128. — Two cavities nests.

CAVITY.	DEPTH OF CAVITY.	DEPTH OF <i>L</i> .	NUMBER OF CELLS.	DEVELOPM. STAGE.
Uppermost.	15 cm		3	3, 3, 4
Middle.	19 cm	25	3	1, 1
Lowest.	20 cm	31	2	0', 1

Judging from the similar age of immature stages in two lower *CC*, the curious branching of *L* and the still half-built *Ca* (Cf. Table 12), this nest seems to offer the most probable example to the second assumption mentioned above, i. e., simultaneous and relatively independent work among nest mates.

III. — IMMATURE STAGES

A considerable number of immature individuals was obtained at the nest excavation. They were brought to the laboratory and either morpho-

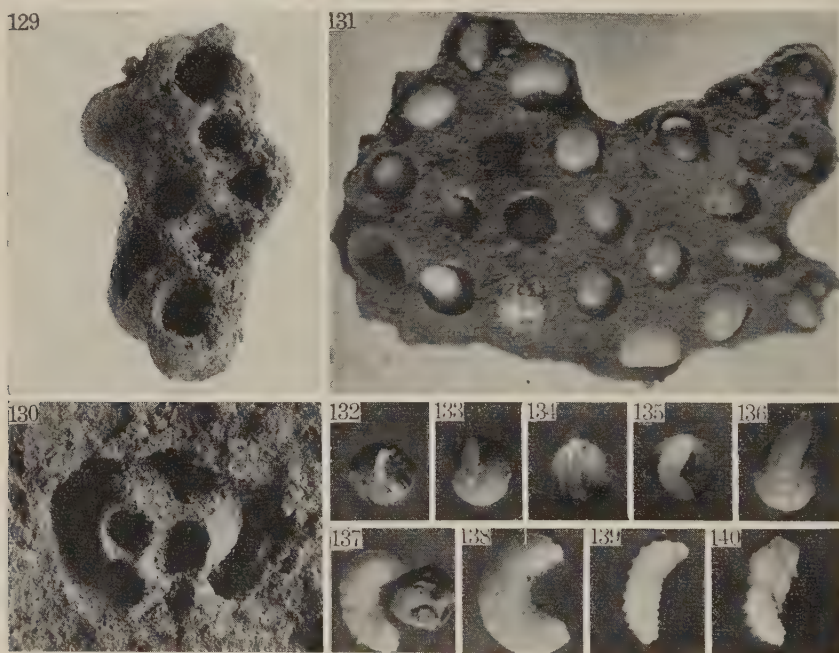


FIG. 129. — A separated empty cluster. FIG. 130. — A cluster within the cavity. FIG. 131. — A separated cluster showing the immature stages within it. FIGS. 132-140. — Immature stages.

logically examined or artificially reared in order to estimate the duration of immature stages. But, the eggs and young larvae were so sensitive to the change of physical conditions that no larvae younger than 4th instar survived under the laboratory conditions. On the other hand, those older than 4th instar were hard enough to maintain alive until emergence.

Histological observations of metamorphosis will be published elsewhere. In this section, some external changes during development are briefly described.

Following the recent advances in knowledge of the external morphology of immature stages of various bees, the description of 4th instar larva and pupa are given, based upon the terminology of Michener (1953, '54).

3. 1. Eggs.

The eggs differ little in form from those of other bees, being milky white, elongate, distinctly curved and attached by the thicker end on the surface of pollen ball (Fig. 132). The thinner end lightly contacts the ball and is directed toward the cell opening. The length is 2.33 to 2.99 mm (Mean 2.54) and the width 0.66 to 0.83 mm (Mean 0.71). The duration of egg stage could not be determined. The eggs brought to the laboratory mostly succumbed without hatching, but some hatched after 1 to 3 days. Judging from the records of eggs of other bees by various authors, the stage is estimated to last approximately 3 to 4 days. Immediately before hatching, the thicker end shows an indistinct shadow.

3. 2. Larvae, general accounts.

Both in hatching out or in moulting, the egg shell or old skin is removed from the anterior part of the body (Fig. 152). The newly hatched out larva eats the pollen ball from the area nearest to its mouth, which results in the formation of a "cleavage furrow" on the ball. Until the 4th instar, they eat only a small quantity, so that the form of the pollen ball is approximately maintained up to this instar, during which about $\frac{2}{3}$ of total quantity is consumed (Fig. 136-137). The rearing of 1st to 3rd instar larvae is extremely difficult. The larvae were put either in a plaster cell or on a cotton layer spread on the bottom of Petri dishes. In spite of the careful control of moisture, they succumbed either to the multiplication of mould or, under drier conditions, by refusing the further feeding. In the later instance, they show often a peculiar body posture with the head raised slightly, as illustrated by Rayment (1937) in *Halictus emeraldensis*. Among more than fifty individuals reared, the duration of each instar was determined only in two instances in 1st instar (both 2 days), one instance in 2nd instar (2 days) and no instance in 3rd and 4th instars. After the consumption of the whole pollen ball, the larvae attain the maximum size, with tightly stretched skin and darkening of body colour due to the accumulation of fecae (Fig. 138). The duration of this predefecation stage lasts 1 to 4 days (Mean 2.2, Mode 2 in 14 cases) and from the defecation to the pupation 1 to 5 days (M. 2.2, Mo. 2 in 27 cases). There is no significant difference in these durations between spring and summer broods under

the room temperature. The manner of defecation is identical to that recorded in *H. quadricinctus* Fabricius by Semichon (1901). When the total food is consumed, the larvae lie on the bottom of cell upside down, with the head directed to the cell opening. Because of the coiled body form, the anus faces the upper posterior corner of the cell. In this posture, they perform a rhythmic longitudinal movement, which results in a fecal streak rubbed against the cell wall (Fig. 153). Through the frequent change of direction during the movement, the posterior wall is finally coated by an ochraceous thick fecal layer, which serves as an indication of successful development even in the empty cells after emergence (Fig. 154). After the defecation, the larvae again becomes paler, with the recovery of segmental constrictions (Fig. 139). Four larval instars are distinguished by the head width, while the maximum body width (usually at the 3rd thoracic segment) grows continuously from instar to instar (Table 16).

TABLE 16. — RELATIVE SIZE DURING LARVAL INSTARS.

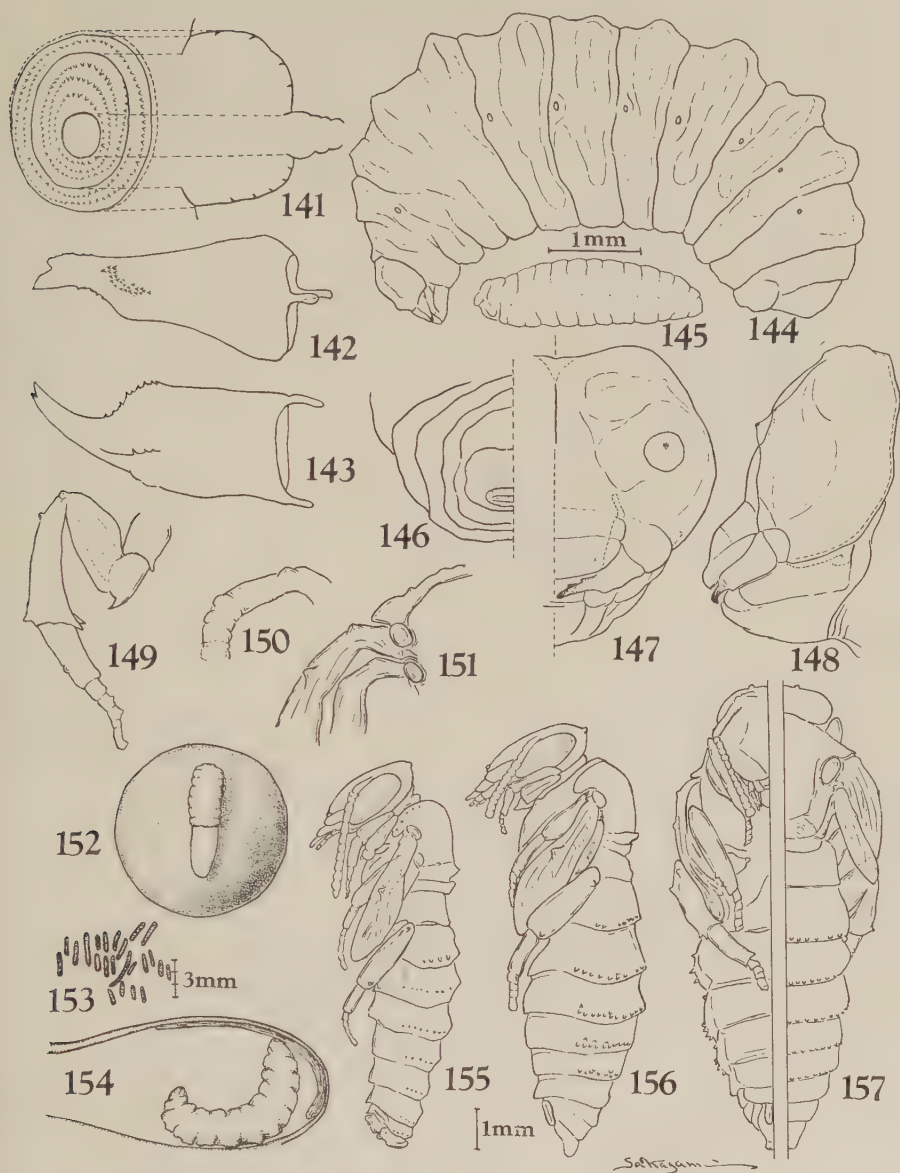
DEVELOPM. DEGREE (*).	LARVAL INSTAR.	HEAD WIDTH.		MAXIMAL BODY WIDTH.	
		Mean.	Range.	Mean.	Range.
2	1	0.59 mm	0.56-0.84 mm	1.25 mm	0.72-1.89 mm
3	2	0.94 mm	0.89-1.00 mm	1.71 mm	1.22-2.22 mm
4	3	1.24 mm	1.17-1.28 mm	2.17 mm	1.50-3.11 mm
5	4	1.54 mm	1.50-1.61 mm	3.41 mm	2.00-5.00 mm

(*) Cf. 2, 3.

3. 3. Description of 4th instar larvae. (Fig. 144-148).

Michener gave descriptions and illustrations of several halictine larvae of *Halictus* and *Lasioglossum*. The following description of 4th instar larvae of *H. duplex*, which belongs to *Lasioglossum* (Subg. *Evyllaues*) in the definition of Michener, was prepared mainly in comparison with that of *L. (Evyllaues) kincaidii* (Cockerell) given by him.

Intersegmental lines distinct except between thoracic segments. Dorsolateral tubercles of thoracic terga, especially of 3rd tergum, distinct with sharp edges, but less conspicuous than in *L. kincaidii*, scarcely extending beyond the spiracular line. Tubercles of abdomen transverse, interrupted distinctly on the medial dorsal line, but after defecation distinct, covering often almost whole lateral side, especially on 1st to 3rd abdominal segments, though slightly narrower and flatter at the spiracular line. Before defecation, tubercles inconspicuous, represented only by a keel-like transverse elevation at the middle of each segment (Cf. Fig. 144). Head capsule (Fig. 147, 148) with neither setae, spicules, nor any other micro-structures. Moderately sclerotized. Posterior tentorial pits invisible from outside



FIGS. 141-157. — Immature stages. FIG. 141. — Larval spiracle. FIGS. 142 and 143. — Larval mandible, inner and ventral views. FIG. 144. — Post-defecation larva. FIG. 145. — First instar larva. FIG. 146. — Larval anal part. FIGS. 147 and 148. — Larval head capsule, frontal and lateral views. FIG. 149. — Fore leg of pupa. FIG. 150. — Basal part of pupal antenna, frontal view. FIG. 151. — Wing base of pupa. FIG. 152. — Hatching out (Posterior half still within egg shell). FIG. 153. — Fecal streaks by mature larva upon glass plate. FIG. 154. — Mature larva coating the cell wall by defecation. FIG. 155 and 156. — Lateral view of male and female pupae. FIG. 157. — Ventral and dorsal views of female pupa.

but represented internally by a short and robust tentorial arm. Head with two round convexities above level of antennae, though flatter than in *L. kincaidii*. Cleavage suture distinct at vertex, gradually changing into a furrow downward until lower frontal convexity. Labral tubercles and edges with minute dark setae. Epistomal suture practically absent. Labroclypeal suture weak. Labrum with a pair of tubercles in both sides, often dark-spotted. Maxillae simple, without palpi. Prementum distinctly exceeding the maxillae. No distinct furrow between pre- and postmentum. Salivary opening minute and inconspicuous, with no lip nor any other peculiar structures. Mandibles with a flat tubercle on outer surface midway between base and apex (Figs. 142-143), the tubercle much less conspicuous than in *L. kincaidii*. Mandible bidentate at apex; outer tooth distinctly longer and sharper than the other; outer margin of apical portion with a few minute teeth at midway; inner margin with a few scattered teeth; cusp multidentate. Mandibular tubercles flat, without setae. Spiracles with several rows of teeth, which are somewhat more conspicuous than in *L. sparsum* illustrated by Michener (Fig. 141). Peritreme collar of primary tracheal opening present but inconspicuous.

3. 4. Pupae.

In Section 2. 3., the pupal stage was distinguished into 12 developmental stages or degrees according to the spread of pigmentation. As in most bee pupae, the pigmentation of body appears only after the eyes become completely black. At first, the inverted U-shaped marking on the mesonotum, and the marginal areas of abdominal terga, then the center of thoracic pleura, begin to darken (Degree 15). This stage is followed by the further darkening (Degree 16) and complete pigmentation of thorax (Degree 17). There is always a distinct delay of the abdominal pigmentation. The tips of antennae and legs become black at the final stage (Degree 19), in which the sclerotization is completed and the pupae differ from the adults practically only by the rudimentary wings. Like as in many halictine bees, *H. duplex* does not spin a cocoon. The pupae are motile throughout the stage, violently shake the abdomen when appropriately stimulated.

The description given below contains the characters peculiar to pupae alone (Michener, 1954) (Figs. 149-151, 155-157): Vertex with pair of protuberances in position of lateral ocelli, no protuberances in front of pronotum distinctly produced but not spined. Scutellum with pair of high protuberances at each side, and with pair of small, inconspicuous ones at the antero-lateral corners. Metanotum with pair of broad protuberances. Middle of each fore-wing with protuberance, smaller one at base of each wing (Fig. 151). Coxae and trochanters each with small spine. Bases of fore-femora each with very inconspicuous protuberance. Outer surfaces of hind tibiae with two small protuberances near base

and apex, the latter weaker (Fig. 149). Number of mesonotal tergal spicules variable, 1 to 5 in females and 1 to 6 in males. Spicules on each abdominal tergum similar to each other, but those in the first and last segment somewhat inconspicuous. Number of abdominal spicules variable namely:

TERGAL NO.	1	2	3	4	5	6
Male.	4-6	8-10	9-10	8-10	5-10	4-8
Female.	4-8	8-12	11-12	11-12	4-8	

The duration of each developmental degree of the pupal stage is given in Table 17. As the total pupal duration in the last column of the table is based upon the data of individuals which could be continuously reared to the emergence, so the values do not always coincide to the sum of days

TABLE 17. — DURATION OF EACH DEVELOPMENTAL DEGREES WITHIN PUPAL STAGE.

SEASON AND SEXES		DEVELOPMENTAL DEGREE (Cf. 2. 3) IN DAYS.								TOTAL PUPAL DURATION IN DAYS.	
		8-9	10	11	12	13-14	15-17	18	19		
Spring Female.	Mx (*)	3	2	2	5	7	6	3	4	m (**)	19.2
	Mo	2	1	2	3	4	2-3	1	2		
	Mn	1	1	1	1	2	1	1	1	v	1.195
	m	2.8	1.3	1.8	2.7	4.2	3.0	1.8	2.2		
	f	8	6	6	8	11	10	7	7	f	9
Spring Male	Mx									(m)	15, 16
	Mo	3	2	2	2	2	2	2	3		
	Mn					1				v	—
	m	3	2	2	2	1.5	2	2	3		
	f	2	2	2	2	2	2	2	2	f	2
Summer Female	Mx	3	1	2	2	5	2	3	?	m	13.5
	Mo	2	1	1	1	3	1	1	2		
	Mn	1	1	1	1	2	1	1		v	2.86
	m	1.9	1.0	1.0	1.1	4.0	1.3	1.5	2.0		
	f	13	13	14	15	31	23	24	16	f	24
Summer Male	Mx	4	2	2	2	6	2	3	5	m	13.2
	Mo	2	1	1	1	4	1	1	2		
	Mn	1	1	1	1	3	1	1	2	v	1.36
	m	1.8	1.1	1.1	1.2	4.2	1.3	1.6	2.4		
	f	18	16	12	15	18	15	12	15	f	15

(*) From above, Maximum, Mode, Minimum, Mean and Number of observations.

(**) From above, Mean, Variance and Number of observations.

given in each developmental degree. Difference of total pupal duration between spring and summer females is highly significant with 1 % fiducial limit, but that between the two sexes in the summer season is insignificant. Although all data were taken at room temperature, the immature stages appear to grow more slowly in spring than in summer under the natural conditions, too; this is shown by the relatively small overlap in seasonal distribution of the stages in spring as compared to that in summer (cf. Sakagami & Hayashida, 1958, Fig. 1).

Because of high mortality among the younger larvae, no concrete estimate of the total duration of the immature stages can be given. The following figures are only an approximation to be corrected through further observation.

DEVELOPM.	0'	0	1	2	3	4	5	6	7	8-9	10	11	12	13-14	15-17	18	19	20	Total.
DEGREE..	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
SPRING ...	1	1	3	2	2	2	2	2	3	3	1	2	3	4	3	2	2	1	39
SUMMER ..	1	1	3	2	2	2	2	2	3	2	1	1	1	4	1	2	2	2	33
	Pollen		Egg		Larva					Pupa					Pre-adult.				

3. 5. Pollen balls.

The preparation of pollen balls is naturally a task of adult females. But it is so intimately connected to the development of immature stages that miscellaneous observations on the pollen balls are touched upon here as the final part of the data in this paper.

The process of pollen ball preparation cannot be directly traced. But the following states were observed among the cells containing still amorphous pollen mass (Degree O₂ in 2. 3.).

1. Cells being full of pollen mass still not moistened by nectar.
2. Cells of which bottom coated by a thin pollen layer.
3. Cells with a flat deposition of thickly pollen-nectar mixture.
4. Cells with a clumsy pollen mass with thickly inside and rather dry surface.
5. Cells with a flat pollen mass with surface elaborated as in the accomplished pollen ball.

The states 2 to 5 seem to represent the gradual elaboration of pollen ball. While the state 1, the most common one among all states mentioned above, cannot be adequately related to others.

The size of pollen ball is highly variable even within one and the same nest. The range of variability was in five summer nests, 54-71, 33-64, 29-70, 64-79, 41-79 mg (in fresh weight) respectively. The mean of 25 balls was 58 mg (variance 13.5) in fresh weight, and 35.7 mg (variance 10.0) in dry weight. An accomplished ball is approximately spherical, slightly flattened on the vertical axis, *fully moulded, or dough-like*, with finely elaborated surface. The longer horizontal axis (length) is parallel

to the longitudinal axis of the brood cell. The ranges of variability of length, width and height are shown in Table 18. There are slight but

TABLE 18. — SIZE OF POLLEN BALLS IN SPRING (P) AND SUMMER (A) SEASONS.

		2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5 mm.
LENGTH	P			1	3	5	9	4	1		
	A				1	6	22	18	21	8	2
WIDTH	P		1		5	2	4				
	A				4	13	30	22	7		
HEIGHT	P	1			2	1	1				
	A		2	7	45	18	9				

significant differences in length and width between spring and summer pollen balls. Legewie (1925) observed a similar tendency in *H. malachurus* Kirby and explained it by several causes, among which the increased foraging ability caused by more than one forager relative to the oviposition rate within the nest seems to be reasonable in *H. duplex*, too.

IV. — CONCLUDING REMARKS

The nest structure of *H. duplex* is summarized as follows: Nests in well insulated, flat, or occasionally slightly inclined, rather hard ground with moderate humidity, without tree and shrub strata and without or with only sparse surface cover. No marked preference to soil types. Nests often forming dense aggregations of more than 20-30 per 1 sq. m. with the minimum inter-nest distance of 1-2 cm.

Spring nest newly excavated by a single post-hibernating mother. Summer nest composite, made by deepening the spring burrow, inhabited by a long-lived mother and her daughters, either fertilized or not. Tumulus radial and central; outer wall rough, inner wall often smooth but without consolidation by saliva. Entrance constricted, 3.5-4.0 mm in diameter, without turret. No special chamber or enlargement immediately below entrance. Depth of main burrow 5-10 to 15 cm in spring and 10-16 to 30 cm in summer, 5-6 mm in diameter, without special enlargement; inner wall fairly smooth, without special lining; general direction vertical, often irregularly bending, without differentiated sections, rarely ramified. Lower blind burrow only exceptionally absent. Lateral burrow usually horizontal or slightly ascending toward cluster cavity, 4-10 mm in length, but often very short, rarely longer than 30 mm,

as wide as main burrow, usually straight, usually opening into the lower half of cluster cavity; inner wall like that of main burrow; depth of connection with main burrow 6-12 cm in spring nests, 15 cm or more in summer ones.

Cell cluster forming typical comb structure, with nearly horizontal cells, which are slightly divergent at back. Surface of cluster smooth, being so elaborated that shape of cells is clearly detectable externally. Occasionally a few marginal cells with irregular orientation. After completion, cluster supported within cavity only at the anterior lower part by several fine pillars or by a few thicker ones. Inter-space between cluster and cavity wall narrow. Cluster formed through excavation, not by building. Number of clusters per nest is 1 in spring nests, 1-2, exceptionally 3, in summer nests. In the summer nests, the later constructed cluster is usually deeper and larger. Spring cluster and lateral burrow become filled with earth after emergence of daughter bees.

Cells elongate oval, bilaterally symmetrical, with undersides flatter, 12-13 mm in length, 6-6.5 mm in maximum diameter and 3-4 mm in neck diameter; Inner wall smooth and polished with thin waxy lining. Pollen ball subspherical, distinctly flattened, dough-like. Defecation on the posterior half of the ceiling of cells. Cell closure or plug loose and permeable. Number of cells usually 3-8 in spring nests, 4-18 in summer, maximum 30 per cluster and 40 per nest. Developmental gradient within cluster progressive and ascending. Distribution of sexes irregular in both spring and summer nests. General order of nest construction not strictly consecutive; comb, cavity, lateral burrow and blind burrow excavated more or less synchronously.

According to the classificatory system of MALYSHEV (1936), the nests of *H. duplex* belong to the *derived honeycomb type of anodalous (independent) nest*, like as that of *H. quadricinctus* Fabricius. However, the senior writer pointed out in another paper (SAKAGAMI and MICHENER, in preparation) that the so-called combed nests of halictine bees, which are characterized by the cluster of closely attached cells and the occurrence of a cavity surrounding them, can be classified into five types (Type IV to VIII). In this system, the nest pattern of *duplex* is placed in Type V, characterized by the cluster-cavity system communicated to the main burrow through a common lateral, of which diameter is nearly as wide as that of the main burrow, and further in Subtype V *b*, characterized by the completely excavated cavity and the horizontally directed cells. The comparison of various types of combed nests found in Halictinae is given fully in the paper mentioned. The nests of *duplex* represent one of the most elaborated types in the subfamily; nevertheless the social organization of this species is not so highly differentiated as in *H. malachurus* Kirby (NOLL, 1931; BONELLI, 1948), *H. marginatus* Brullé (QUÉNU, 1955-1957), and *H. rhytidiphorum* (Loure) (MICHENER et LANGE, 1958), which all make relatively simple branched nests without comb-cluster system. The differentiation of social organization and architecture must

be separately studied, although they may be closely related to one another.

Finally, the writers should like to express their heartiest thanks to Prof. TOHRU UCHIDA of *Zoological Institute, Hokkaido University* and Prof. CHARLES D. MICHENER of *Department of Entomology, University of Kansas* for their kind direction and encouragement of this work. Their sincere thanks are also due to Mrs. C. PLATEAUX-QUÉNU (formerly, Miss. QUÉNU) of *Laboratoire d'Évolution, Paris*, for her kindness shown to their works.

Summary.

In the present paper, the nest structure of *Halictus duplex* Dalla Torre was described in detail, from both static and dynamic aspects, together with descriptions of immature stages. This comb-making species shows the highest degree of architectural development, nevertheless its social differentiation is not so high as in *H. malachurus* Kirby and *H. marginatus* Brullé, nests of which remain still in a less developed stage.

Zusammenfassung.

In der vorliegenden Arbeit, wurden die Beschreibungen des Nestbaues von *Halictus duplex* Dalla Torre ausführlich gegeben, sowohl statisch als auch dynamisch, nebst die Beschreibungen der Entwicklungsstadien. Diese wabenerzeugende Art zeigt baukünstig den höchsten Entwicklungsgrad, obgleich ihre soziale Differenzierung nicht so hoch ist wie bei *H. malachurus* Kirby und *H. marginatus* Brullé, deren Nester noch in einem ursprünglicheren Zustand bleiben.

Résumé.

Cet article concerne la structure du nid de *Halictus duplex* Dalla Torre, envisagée sous un double aspect statique et dynamique. Les stades pré-imaginaux de cette espèce sont également décrits. *Halictus duplex*, dont le nid montre une complexité architecturale poussée au plus haut point, n'atteint pas, cependant, un degré de différenciation sociale aussi élevé que *Halictus malachurus* Kirby et *Halictus marginatus* Brullé dont les nids sont de type beaucoup plus simple.

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